University of Alberta

Limits on the Exploitation of the Yucca-Yucca moth Mutualism

by

M. Lynne James ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring 1998

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-28950-8

Canadä

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read the thesis, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Limits on the Exploitation of the Yucca-Yucca Moth Mutualism** submitted by **M. Lynne James** in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

Dr. John F. Addicott (Supervisor)

Dr. Susan Hannon (Committee Chair)

Jens Roland

Dr. Jens Roland (Committee Member)

Dr. Eric Higgs (Committee Member
and External Examiner)

22 January, 1998

Abstract

The mutualism between a yucca (*Yucca kanabensis)* and its pollinators (*Tegeticula yuccasella* spp.) is exploited by a non-pollinating yucca moth which decreases yucca seed set by 30%. My objective for this study was to determine the role of three potential limits in limiting the exploitation of the yucca-yucca moth mutualism by the non-pollinator. I found that the interspecific competition between pollinator and non-pollinator larvae for yucca seeds was the strongest limit to exploitation. In fruit with both pollinator larvae, non-pollinator larval survival decreased sharply. However, exploitation was not limited through density dependent population regulation of the non-pollinator, as noticeable intraspecific competition between non-pollinator larvae was rare. Finally, isolation of yuccas in time and space from non-pollinators was a moderate, but inconsistent limit to exploitation because: a) few plants were isolated enough in space to prevent non-pollinators from discovering them, and b) plants do not consistently escape in time, because of the variation in flowering and non-pollinator emergence times between years.

Acknowledgements

I thank my supervisor, John Addicott, for his guidance and for the opportunity to leve and work in Kanab. I thank my committee members, Jens Roland, and Randy Currah for their input through the course of this project. I am grateful to Eric Higgs, for joining my committee, and to Susan Hannon for reading my thesis and chairing my defense. I also thank all of the members of the Yucca lab, past and present - Shelley Humphries, Julius Csotonyi, Alina Fischer, Tan Bao and Reid Wilson - for field assistance and helpful discussions. Above all, I thank my family, my friends, and my husband, Adam James, for their support.

Table of Contents

Page #

Abstract

Acknowledgments

List of Tables

List of Figures

Chapter 1. Introduction 1

Overview.. 1

The Evolution of Mutualism.. 1

Cheating.. 5

Exploitation of Mutualisms... 7

Limits on the Impact of Exploitation.................................... 8

The Yucca-Yucca Moth Mutualism..................................... 12

Literature Cited.. 18

Chapter 2. The Role of Mutualists in Limiting Exploitation...................... 23

Abstract.. 23

Introduction.. 23

Materials and Methods.. 26

Results.. 32

Discussion.. 33

Literature Cited.. 40

Chapter 3: Intraspecific Competition and Non-Pollinator Oviposition Patterns 57

Abstract.. 57

Introduction.. 57

  - Materials and Methods........ 61
  - Results........ 65
  - Discussion........ 68
  - Literature Cited........ 76
- Chapter 4: Life History Synchronization and Yucca Population Structure 93
  - Abstract........ 93
  - Introduction........ 93
  - Methods........ 98
  - Results........ 102
  - Discussion........ 104
  - Literature Cited........ 112
- Chapter 5: Summary........ 124
  - Overview........ 124
  - Major Findings and Future Work........ 125
  - Conclusions........ 130
  - Literature Cited........ 132

List of Tables

Table 2.1 Age of fruit with droplets and without droplets. 45

Table 3.1 Intraspecific competition in non-pollinators of all instar stages......... 80

Table 4.1 Factors influencing the presence of droplets in fruit..................... 116

Table 4.2 Factors influencing the number of droplets in fruit 116

List of Figures

Figure 2.1 Proportion of seeds eaten by non-pollinators.............................. 46

Figure 2.2 Fruit retention as a function of droplets.................................. 47

Figure 2.3 Age of fruit with and without droplets.................................. 48

Figure 2.4 Cumulative probability of fruit abscission.............................. 49

Figure 2.5 Probability of survival versus the number of pollinators in 1995....... 50

Figure 2.6 Probability of survival to 12 days versus number of pollinators...... 51

Figure 2.7 Probability of survival to 28 days versus number of pollinators...... 52

Figure 2.8 Probability of survival in feeding tunnel.................................. 53

Figure 2.9 Seeds eaten versus larvae in locule.. 54

Figure 2.10 Weight of non-pollinators versus larvae per locule....................... 55

Figure 2.11 Ovipositions versus pollinators per locule................................ 56

Figure 3.1 Distribution of droplets on fruit.. 81

Figure 3.2 Distribution of droplets on fruit over time................................ 82

Figure 3.3 Distribution of ovipositions in fruit.. 83

Figure 3.4 Distribution of ovipositions in locules...................................... 84

Figure 3.5 Distribution of non-pollinator larvae in fruit............................... 85

Figure 3.6 Fruit choice by non-pollinators... 86

Figure 3.7 Intraspecific competition of non-pollinators in 5 developmental stages.. 87

Figure 3.8 Probability of survival to 28 days versus fruit age and ovipositions.... 88

Figure 3.9 Probability of survival to 12 days versus fruit age and ovipositions.... 89

Figure 3.10 Probability of survival versus ovipositions in observation fruit...... 90

Figure 3.11 Weight of non-pollinators versus non-pollinators per locule......... 91

Figure 3.12 Seeds eaten per larvae versus number of non-pollinators per locule... 92

Figure 4.1 Survival of male and female non-pollinators............................. 116

Figure 4.2 Frequency of flowers and fruit at male and female emergence in 1995 117

Figure 4.3 Frequency of flowers and fruit at male and female emergence in 1996 118

Figure 4.4 Flowers and fruit per plant at male and female emergence.............. 119

Figure 4.5 Proportion of fruit with droplets on isolated and control plants........ 120

Figure 4.6 Ovipositions per fruit on isolated and control plants..................... 121

Figure 4.7 Probability of droplets versus flowering date and fruit number......... 122

Figure 4.8 Map of 1996 spatial observation site......................................

Chapter 1

Introduction

Overview

Recently, there has been heightened interest in quantifying the impact of exploiters on mutualistic systems (Morris 1996; Kerdelhue and Rasplus 1996; Bultman and Mathews 1996). However, very few studies have focused on mechanisms which limit the impact of the exploitation of mutualisms (but see Turner et. al. 1984). For my M.Sc. thesis, I examined the role of potential limits to exploitation of mutualisms, by studying the ecology of a moth that exploits the yucca-yucca moth mutualism.

In this chapter, I provide the conceptual background for the problem. I begin by introducing the concepts of cooperation and mutualism, and discuss five possible mechanisms for the evolution of mutualism. I then consider the concepts of cheating and exploitation in mutualistic systems, and discuss some of the processes that can limit exploitation in mutualistic systems. Next, I describe my study system, the yucca-yucca moth mutualism and the moths that exploit it. Finally, I discuss possible limits to the exploitation of the yucca-yucca moth mutualism, and develop the three hypotheses that form the basis for my study: 1) exploitation is limited by the mutualists, 2) exploitation is limited by population regulation of the exploiter, and 3) the exploitation of yucca plants is limited if they are isolated from non-pollinators in time and space.

The Evolution of Mutualism

Interactions which are beneficial to all participants (cooperation and mutualism) occur commonly (Bronstein 1994). ‘Cooperation’ usually refers to interactions among members of one species, and ‘mutualism’ usually refers to interactions between species, although 'cooperation' is sometimes used in reference to interspecific interactions as well (Mesterton-Gibbons 1992). Regardless, the individuals that participate in these interactions grow, survive, and/or reproduce at a higher rate when in the presence of a cooperator or mutualist than when alone (Boucher et. al. 1982).

Cooperation has been the focus of much recent evolutionary and behavioural study (eg. Axelrod and Hamilton 1981; Axelrod and Dion 1988; Wilkinson 1984; Milinski 1987). The reason for this interest is that cooperation and mutualism appear to present a paradox. Organisms are not expected to cooperate at their own expense; instead, because the individual is widely accepted as the unit of selection (Doolittle et. al. 1980; Alexander and Borgia 1978), they are expected to behave selfishly. Depite the apparent conflict between the inherent selfish nature of organisms, and cooperative behaviour, there are at least five hypotheses for how cooperation and mutualism could arise - kin selection, reciprocal altruism, evolution of avirulence, by-product mutualism, and group selection.

Cooperation Among Related Individuals

One of the strongest models for the evolution of cooperation is the application of kin selection theory (see Axelrod and Hamilton 1981; Dugatkin 1997). In kin selection, organisms may behave in an apparently altruistic manner, helping relatives rear young at the expense of their own reproduction (Hamilton 1964). An excellent example of kin selection occurs in the eusocial naked mole-rat (Jarvis 1981; Jarvis et al. 1994; reviewed in Dugatkin 1997) in which a large group has a single queen, one to three reproductive males, and a large number of nonreproductive males and females which maintain and defend the colony. In a less extreme case, the altruistic behaviour of young Florida scrub jays may also be explained by kin selection. Here, the sons of a breeding pair will not breed, but instead will remain at the parental nest and help their parents rear their young (Mumme 1994; and Woolfenden 1984). In both cases, the workers are closely related to the young they help rear, and helping the parents or queens produce extra siblings has the same genetic consequences as rearing young of their own (Hamilton 1964; Jarvis 1981; Woolfenden 1984; Ridley 1993).

Cooperation Between Unrelated Individuals

Cooperation between unrelated individuals is more difficult to explain than cooperation between related individuals, since there could potentially be no benefit in "helping" a very distant relative, or a member of another species. There are, however, several theories to explain the evolution of cooperation and mutualism under different circumstances (Mesterton-Gibbons 1992; Connor 1995; Axelrod and Hamilton 1981; Axelrod and Dion 1988; Wilson 1990).

The most celebrated theory of cooperation is the theory of reciprocal altruism (Trivers 1971; Axelrod and Hamilton 1981). In 1981, Axelrod and Hamilton put forth a theory of evolution of cooperation based on the Prisoner's Dilemma. In the Prisoner's Dilemma game, two players meet and can choose between two strategies C, to cooperate, and D, to defect. If both players cooperate, their payoff is R, which is higher than P, the payoff if they both defect. However, the payoff to a player who unilaterally defects, T, is greater than R, while the opponent ends up with S (the sucker's payoff), which is less than P. In addition to this $T>R>P>S$ ordering, it is also assumed that $2R>S+T$. Axelrod and Hamilton (1981) found that in a iterated Prisoner's dilemma game in which the players had a high probability of meeting again, a strategy called TIT FOR TAT did exceptionally well. This strategy was very simple: a player cooperated on the first move, and copied its partners last choice on every other move. The strategy was found to be robust, stable, and initially viable under the conditions of the game (Axelrod and Hamilton 1981).

Recent modifications of the Iterated Prisoner's Dilemma model allow more than two partners to interact, allow the players to either opt out or ostracize other players, adjust the payoff schedule, and allow players to take into account the previous actions of other players (Axelrod and Dion 1988; Nowak and Sigmund 1993). These models show other possible strategies for the evolution of cooperation including Generous TIT FOR TAT, and "win-stay, lose-shift", which are more robust than TIT FOR TAT under certain conditions (Nowak and Sigmund 1993a and 1993b).

There are several excellent examples of organisms using a tit-for-tat strategy (Milinski 1987; Wilkinson 1984; Dugatkin 1991; Hart and Hart 1992). Perhaps the most famous example is of three-spined sticklebacks using reciprocal altruism during cooperative predator inspection visits. In an elegant experiment, Milinski demonstrated that sticklebacks that were inspecting predators were more likely to behave in a cooperative manner when they perceived that there was another stickleback helping them inspect the predator, than when they perceived that another fish was 'defecting' and straggling behind (Milinski 1987).

Reciprocal altruism is the most famous path to mutualism and cooperation, but it is not the only one. In fact, by-product mutualism may actually be the most common route to mutualism (Mesterton-Gibbons 1992; Connor 1995; Dugatkin 1997). By-product mutualisms originate when one or both parties 'incidentally' benefit from the selfish behaviour of others, and as such incur no cost in the association. Examples of by-product mutualism include mixed species flocks of birds or schools of fish, or Müllerian mimicry in which organisms benefit simply from the presence of other organisms because they either deflect the attention of predators, or help to train predators (Connor 1995; Turner et. al. 1984; Turner 1987).

A third path toward cooperation between unrelated individuals may be through the evolution of avirulence between a host and a parasite (Connor 1995; Thompson 1982). Mutualisms may arise between hosts and parasites in two ways. First, a parasite may confer a by-product benefit to its host which is greater than the cost it inflicts. A good example of this is in insect-pollination mutualisms, in which pollination occurred as a by-product of insects feeding on pollen (Connor 1995). Second, a parasite may be selected to either become less harmful to the host, or provide the host with a resource or service such as protection, if an increase in host health, survival or reproduction also benefits the parasite (Connor 1995).

Finally, cooperation and mutualism may evolve through group selection (Dugatkin 1997; Mesterton-Gibbons 1992; Wilson 1990). In this controversial scenario, cooperation or mutualism can evolve even when individual mutualists are at a disadvantage compared to nonmutualists, as long as groups with mutualists are more productive than groups without mutualists (Wilson 1980; Wilson and Sober 1994; reviewed in Dugatkin 1997). One potential example of group selection may be in the ant, *Messor pergandei*, in which cooperation between the many unrelated queen foundresses of a colony increases the number of workers in the colony (Rissing et. al. 1991).

Cheating

In kin selection, organisms truly cooperate with other organisms at their own (short term) expense. In other instances of cooperation and mutualism, however, the relationship appears to be nothing more than mutual exploitation in which both partners happen to benefit (Bronstein 1994). Because of the inherent selfish nature of all organisms, if there is a cost to mutualism that can be avoided, an organism will cheat. Cheaters, then, are defined as an individual of a species involved in a mutualism that receives the benefits of mutualism but does not reciprocate (Soberon and Martinez 1985).

The mechanisms that promote cheating behaviour are the reverse of those which promote mutualistic behaviour. First, cheating is most likely to occur in systems in which there is a cost to mutualistic behaviour, which cheaters can avoid (Soberon and Martinez 1985; Dugatkin 1997). For example, in many plant-pollinator interactions, the most efficient way for the pollinator to access the nectar or pollen reward is by pollinating the plant, so cheating is not expected to arise. The plant, on the other hand, expends energy producing nectar, and might benefit by not producing nectar if it was still pollinated. Indeed, there are several systems in which some plants of a species do not produce nectar (Feinsinger 1978), but still benefit from pollination (Feinsinger 1983).

Second, mutualism is more likely to occur in systems where individuals can recognize each other and punish each other for cheating, and therefore cheating is facilitated when recognition between individuals is poor (Soberon and Martinez 1985; Boyden 1982). For example, some species of flowers produce variable nectar rewards; some produce a large quantity of nectar, while others produce none. Those that produce no nectar are cheaters, and take advantage of the fact that their pollinators cannot distinguish them from the nectar producers, and therefore do not avoid them (Feinsinger 1978, 1983; Pyke 1981).

Third, when there is a high probability that two individuals will meet again, mutualism is favoured, while cheating is promoted when individuals are unlikely to meet again (Trivers 1971; Axelrod and Hamilton 1981). The latter occurs when either one or both species is short-lived, or when the cheater is mobile (Enquist and Leimar 1993; Houston 1993; but see Ferriere and Michod 1996). Often, these two things are related to recognition. Bawa (1980) demonstrated that long-lived animals with spatial memory and sight, such as hummingbirds and butterflies, ignore the nectarless female flowers *Carica papaya* and *Jacaratia dolichaula*. Sphingid moths, on the other hand, which approach the flowers with olfactory cues, pollinate them because they cannot distinguish between male and female flowers.

Finally, cheating is promoted when there is a large disparity between the time a reward is produced, and the time a partner receives a reward. The reward that was produced first can be exploited by a cheater (Axelrod and Hamilton 1981; Soberon and Martinez 1985). The best example of this is in pollination systems, where the plant incurs the cost of mutualism (nectar production) before it is pollinated. If the plant produced nectar at the same time it was pollinated, there would be no opportunity for it to be exploited by nectar robbers (Soberon and Martinez 1985).

Exploitation of Mutualisms

Cheating by members of mutualistic species is only one process that may threaten or destabilize a mutualism. A second process that may damage the relationship between mutualists is exploitation by members of species which never participate in the mutualism, but who nonetheless benefit from a mutualism (Soberon and Martinez 1985). Two groups of exploiters have been identified, and their classification depends on the nature of the relationship between the exploiter and both mutualists. Type 1 exploiters benefit from both partners in a mutualism. Most Type 1 exploiters are mimics which benefit by taking the form of one (or both) mutualists(s). Batesian mimics (Turner et al. 1984; Turner 1987), Peckhammian mimics (Soberon and Martinez 1985; Losey 1972; Gorlick et al. 1978; Louda 1982; Rettenmyer 1970), and species of nectarless flowers which mimic nectar-producing flowers (Dafni and Ivri 1981; Dafni 1983; Dafni 1984) are all Type 1 exploiters. Another example is the *Phyllobaenus* beetle which exploits an unusual mutualism between plants in the genus *Piper* and an ant, *Pheidole bicornis*. In this case, the beetle exploits both mutualists by feeding on the food bodies produced by the plant and on the ant brood (Letourneau 1990, 1991).

Type II exploiters, on the other hand, benefit from one of the mutualists, but sustains a cost by associating with the other (Soberon and Martinez 1985). The cost of invading the mutualism may be the reason why Type II exploiters are rarer than Type I exploiters (Soberon and Martinez 1985). There are very few documented examples of Type II exploiters, which include nectar robbers which rob plant nectar, but have to compete with legitimate pollinators for the nectar (Roubik 1982; Roubik et al. 1985). In this case, pollinators may not only visit a flower and consume the nectar before the nectar robbers arrive that day, they may also pollinate the flower, preventing it from producing nectar in the future.

Impact of Exploitation

The impact of exploitation of mutualisms either by cheaters or exploiters ranges widely from strongly negative to neutral. The negative impacts of cheating and exploitation have been demonstrated either empirically or theoretically in many systems. For example, the exploitation of plant-pollinator interactions is often costly to both mutualists. The non-pollinating wasps that exploit the obligate fig-fig wasp mutualism have a negative effect on fig wasp development, and the pollen dispersal of the fig (Kerdelhue and Rasplus 1996; West and Herre 1994). As well, Roubik (1982) found that nectar robbing by the aggressive bee, *Trigona ferricauda* had negative affects on both plant seed set and the foraging of the hummingbird that pollinated it. Further, theoretical studies have shown that Batesian mimics likely increase the risk of predation suffered by mutualistic Muellerian mimics in a frequency-dependent way (Turner et al. 1984; Turner 1987).

On the other hand, Morris (1996) could find no evidence that cheating by nectar robbing bumblebees had any negative effect on either seed set or pollen dispersal of bluebells. It is also possible that other nectar robbers which do not damage flowers, consume much nectar, nor interfere with pollinators, have a very limited impact on pollination systems (Inouye 1980).

Limits on the Impact of Exploitation

In some systems exploitation may be so severe that the mutualism is disrupted. In other mutualisms with a potentially very destructive exploiter, there may be processes that limit exploitation. Three processes that may limit exploitation of mutualisms are: 1) limits by the mutualists, 2) regulation by the exploiters, and 3) escape in space and time by the mutualists.

Limits by mutualists

Mutualists may regulate exploitation by limiting access of exploiters to their resources, or by limiting exploiter numbers. To limit exploiter access to resources, mutualists use a variety of morphological, chemical or behavioural defenses. For example, in pollination systems nectar robbers may either pierce the calyx of flowers, or slip between flower petals to gather nectar without touching the reproductive parts of the plant (reviewed in Inouye 1980, 1983). To limit the impact of nectar robbers, flowers at high risk often have thickened calyxes that are difficult to pierce (Inouye 1983), long, fused corollas (Inouye 1983), and nectar with chemicals benign to pollinators but toxic to exploiters (Stevenson 1981, 1982; Prys-Jones 1992).

Mutualists also reduce the impact of exploitation by lowering exploiter numbers through interspecific competition for mutualistic resources. Mutualists may lower exploiter numbers directly by killing them or evicting them from the area, or indirectly, by depleting mutualistic resources and forcing exploiters to go elsewhere. Competition for mutualistic resources occurs between the hummingbird pollinator and the *Trigona* bee nectar robber of the shrub, *Pavonia dasypetala* (Roubik 1982). In this system both the pollinator and the nectar robber can completely deplete the nectar of a flower, and if the hummingbird pollinates the flower, the flower ceases to produce nectar. Extreme interspecific competition between exploiters and mutualists exists in the ant-acacia mutualisms in Central America (Janzen 1975). Exploiter ants, *Pseudomyrmex nigropilosa*, live in swollen thorn acacias and feed on the beltian bodies produced by the acacia, but do not protect them from herbivores or encroaching vegetation. When the mutualistic acacia-ants discover acacias containing *P. nigropilosa*, they kill or chase out the exploiters within hours.

Regulation by Exploiters

There may be mechanisms by which the impact of exploiters on mutualists is limited by the exploiters themselves, particularly if they are highly dependent on mutualists for their survival and reproduction. One way they may limit their impact is through intraspecific competition for the resources of the mutualist. No one has looked specifically at intraspecific competition between exploiters as a mechanism for limiting exploiter impact, but any density-dependent control of exploiters should limit the exploitation of mutualisms.

While there are no data on density-dependent limits to exploitation, there are studies of the effect of frequency-dependence of exploiters in mutualistic systems (Turner at al. 1984; Turner 1987; Alexandersson and Agren 1996). Batesian mimics, which take advantage of protection from predation provided by Müllerian mimics are considered to be "selected for low density" (Turner et al 1984; Turner 1987). Here, Müllerian mimics are avoided by predators because they are either distasteful or poisonous, and predators learn to avoid them. As the frequency of Batesian mimics increases, predators learn to associate that shape, pattern or colour with food rather than poison, and as a result, predation on both Müllerian and Batesian mimics increases. Studies of similar phenomena in nectarless flower mimics, test the hypothesis that pollination of mimics decreases as their frequency increases because pollinators learn to avoid them. However, results of these studies are inconclusive (Alexandersson and Agren 1996).

Isolation of Mutualists in Time and Space

a) Synchronization of Life Histories

While the impact of exploiters may be limited directly through inter- or intraspecific competition, regulation may be achieved indirectly as well. The interaction of the life histories of several different organisms may itself be a limiting mechanism because if the mutualists and exploiters interact only briefly, exploiters have a limited time to find and use the mutualists. For example, Louda (1982) studied the effect of predation by the spider *Peucetia viridans* on the pollinators and seed predators of the spider's host plant, *Happlopappus venetus*. In particular, Louda examined the effect of the timing of spider predation on the seed set of the host plant. When spiders were present early in the flowering season, they killed a high proportion of the pollinators, but enough pollinators reached the plant to effect pollination. However, because seed predators had access to seed later in the season, the result was a net decrease in seed set. Conversely, when spiders were present later in the season, more pollinators reached the plant and seed predators were eaten, resulting in a net increase in seed production. Louda showed that there was a short window of time in which the interaction between the spider and the plant was mutualistic, and provided a clear example of how synchronization of life history traits can affect the nature of an interaction. In addition, the exploiting seed predators have a very short period of time (after pollination, but before spiders arrive) in which they can exploit the mutualism. As a result of this time constraint, exploitation is limited.

b) Population Structure

Wilson (1983) demonstrated that the structure of a population can promote the evolution of mutualisms because different groups within a population have different abilities to support nonmutualists. He argued that the ability of a population to support nonmutualists was dependent on factors including initial group size, variance in mating success within the group, and dispersal of organisms. Little work has been done to examine the effect of population structure on the ability of mutualists to support nonmutualists, but it is an important avenue to explore. For example, the dispersal of mutualists may result in a heterogeneous distribution of mutualists, some of which are accessible to exploiters, and others which are not. This distribution may force exploiters to focus on particular mutualists, or groups of mutualists, while ignoring others completely. The end result may be to lower the fitness of some mutualists, yet significantly increase the fitness of others, and ultimately allow at least some to reproduce successfully. The end result of this patchy distribution of mutualists may be to limit the impact of exploitation on the populations of mutualists as a whole.

Recently, there has been heightened interest in quantifying the impact of exploiters on mutualistic systems (Morris 1996; Kerdelhue and Rasplus 1996; Bultman and Mathews 1996). However, very few studies have focused on mechanisms which limit the impact of the exploitation of mutualisms (but see Turner et. al. 1984). For my M.Sc. thesis, I examine the role of the above potential limits to exploitation of mutualisms, by studying the ecology of a non-pollinating moth that exploits the yucca-yucca moth mutualism. In particular, I examine the role of the mutualists, the exploiter, and the distribution of yuccas in time and space in limiting the impact of the non-pollinating moth on the yucca-yucca moth mutualism.

The Yucca-Yucca Moth Mutualism

The yucca-yucca moth mutualism is an obligate pollination-seed predation mutualism between plants of the genus *Yucca* and moths of the genera *Tegeticula* and *Parategeticula* (reviewed in Baker 1986). Yuccas are pollinated nearly exclusively by the nocturnal yucca moths (but see Dodd and Linhart 1994). In turn, the larvae of the yucca moths exclusively eat the reproductive tissues of the yucca fruit, and the adult moths appear to mate and rest only in yucca flowers (reviewed in Baker 1986; Riley 1892; Dodd and Linhart 1994).

The interaction between yuccas and yucca moths begins in late spring when yucca moths emerge from the soil and fly to a flower in a yucca inflorescence to mate (reviewed in Baker 1986; Riley 1892; Addicott et al. 1990). Following copulation, females gather pollen in maxillary tentacles which are specialized for the collection and transfer of pollen (reviewed in Addicott et al. 1990; reviewed in Baker 1986). Once pollen is collected, the moth flies to another inflorescence where she oviposits in the ovary of a yucca flower (Aker and Udovic 1981). Following oviposition, she usually pollinates the flower by inserting her maxillary tentacles into the stigma and actively transferring pollen (Tyre and Addicott 1993; Addicott and Tyre 1995). Often, the moth oviposits more than once in the flower, with subsequent ovipositions less frequently followed by pollination (Aker and Udovic 1981; Addicott and Tyre 1995).

Yucca moth larvae hatch from the eggs approximately 9 days following oviposition and begin feeding on the seeds of the developing fruit (Fuller 1990; personal observations). When larvae reach the fourth and final instar, they exit the fruit, drop to the ground, and burrow 5-20 cm into the ground (Fuller 1990). Here they construct a cocoon in which they enter diapause for the winter. Pupation occurs several weeks before the adults emerge in the spring (Fuller 1990).

The yucca-yucca moth mutualism is subject to exploitation by both cheaters and exploiters (Addicott and Tyre 1995; Tyre and Addicott 1993; Aker and Udovic 1981; Addicott 1996; Pellmyr 1996). Cheaters are individuals of the pollinating moths which oviposit without pollinating. Cheating appears to be common in this system, with moths failing to attempt pollination about 25% of the time (Tyre and Addicott 1993). Moths may benefit from cheating by reducing the time spent in one flower, and they therefore may lay more eggs, or may not have to collect more pollen. However, there are risks associated with cheating since flowers that are not pollinated are abscised by the yucca plant (Aker and Udovic 1981). Even if flowers were not abscised, without pollination they would fail to set the seeds on which the moth larvae feed. Thus, cheating can only be a successful strategy if the flower has been, or is likely to be, pollinated by a mutualistic moth.

But even if the moths do pollinate the flowers, they may overexploit the flowers by laying so many eggs that few if any of the seeds survive. Over-exploitation of this kind is also regulated by the yucca. Yuccas are usually resource limited; regardless of the number of flowers that are initiated as fruit, fruit production is limited to less than 10% of total flowers (Udovic 1981; Udovic and Aker 1981; Addicott 1998). In some species of yuccas, flowers with high numbers of ovipositions are selectively abscised (Pellmyr and Huth 1994; Richter and Weiss 1995; Addicott 1998). Together, abortion of flowers that either have not been pollinated, or that have many ovipositions, may limit cheating by yucca moths, because moths are forced to pollinate most of the time, and forced to spread their eggs among many flowers.

Exploiters of the Yucca-Yucca Moth System

The mutualism between some yuccas and yucca moths is exploited by a non-pollinating moth (reviewed in Addicott et al. 1990). Non-pollinators are very similar to yucca moths, except that they are about 50% larger, have rudimentary maxillary tentacles and therefore cannot carry pollen. They emerge about three weeks later in the flowering season, and oviposit in yucca fruit rather than flowers (Addicott et al. 1990; Addicott 1996; Pellmyr et al. 1996). The non-pollinators appear to be derived from pollinating yucca moths, and are considered to be distinct species, but their taxonomy has not been determined (Pellmyr et al. 1996).

Non-pollinators may have a significant impact on the yucca-yucca moth mutualism over ecological and evolutionary time for two reasons. First, they may lay enough eggs in a yucca fruit that the larvae consume all of the seeds (Addicott 1996; Pellmyr 1996). Second, they are less likely to be controlled by selective abscission because they lay eggs in older fruit that are less likely to be aborted. High numbers of non-pollinators, therefore, have the potential to severely reduce yucca seed set and limit sexual reproduction of yuccas.

Since yuccas are long-lived and reproduce by cloning (Kingsolver 1986), non-pollinators likely cause little change in the size of yucca populations over the short term. They may, however, change the complexion of a yucca population over both ecological and evolutionary time. By eating yucca seeds, non-pollinators decrease seed set in yuccas, and may limit the recruitment of seedlings into the population. Also, by focusing activity on particular yuccas, they may differentially affect seed set in yuccas, allowing some plants to contribute seedlings to the population, but not others.

Also over evolutionary time, a severe reduction of yucca seed production may make the population less able to colonize new areas, because yucca dispersal and colonization is done through seeds (Kingsolver 1986). Any reduction in local yucca populations would have a devastating impact on yucca moths and nonpollinators, unless they were able to disperse to areas with more yuccas. Severe exploitation may also select for mutualists with traits that limit the impact of non-pollinators, thereby directing the evolution of yuccas and their pollinators.

The Study System

I studied the processes that limit exploitation of *Yucca kanabensis* (McKelvey) and its two mutualistic moths, (*Tegeticula yuccasella* spp. (Riley)), by a non-pollinating moth (*T. yuccasella* spp.). My study took place near Kanab, Kane County, Utah, USA at two study sites. One site was on the north side of the old US Highway 89 between Kanab and Mt. Carmel Junction (11236’30’’W, 37 10’15’’N). The second site was along the road to Coral Pink Sand Dunes State Park (112 40’45’’W, 37 7’30N). On these sandy sites, the dominant vegetation includes *Y. kanabensis*, *Juniperus monosperma*, *Artemesia tridentata*, *Wyethia scabra*, and *Quercus gambellii* (Addicott and Tyre 1995).

The Questions

In this study, I examine three processes that might limit the exploitation by the non-pollinating moth. In Chapter 2, I ask if the impact of non-pollinators in the yucca-yucca moth system may be controlled by the mutualists. I address the hypotheses that yuccas may limit exploitation through the abortion of fruit, selective or not, and that yucca moth larvae may limit exploitation by competing with nonpollinator larvae for food. Yucca moths lay eggs in fresh yucca flowers, while non-pollinators lay eggs in 2-3 week old fruit. This 2-3 week head start gives yucca moths a competitive advantage over non-pollinators, as they can eat seeds before non-pollinators hatch, and even consume some non-pollinator eggs and young larvae in the process.

In Chapter 3, I ask if non-pollinators limit their own exploitation through intraspecific competition, or conversely enhance their ability to exploit yuccas by spreading out their ovipositions among fruit. Strong intraspecific competition between non-pollinators in fruit may regulate non-pollinator numbers, and ultimately limit their impact on the mutualism. Indeed, preliminary studies have found as many as 50 non-pollinator larvae in a fruit (Addicott 1996), while it takes only about 18 larvae to destroy all of the seeds. If the larvae destroy all of the seeds in a fruit, they may either die of starvation before they emerge, or be lighter at emergence, with less chance of overwintering. On the other hand, intraspecific competition may not be a strong regulating factor if non-pollinators spread their ovipositions evenly among fruit. By spreading their eggs evenly, the impact on any one fruit may be lowered, but because intraspecific competition will be reduced with a rise in non-pollinator survivorship, the impact on the yucca population will be higher.

In Chapter 4, I ask if the extent to which non-pollinators exploit or ignore certain yucca plants is influenced by the distribution of yucca plants in space and time. The timing of yucca flowering may influence the degree to which plants are exploited, because the need for synchronization of the life histories of yuccas, pollinators and non-pollinators may limit the length of time in which non-pollinators may exploit the mutualism. Non-pollinators oviposit in yucca fruit, but also rest in yucca flowers. If non-pollinators emerge too early, they will have no fruit to oviposit in, and if they emerge too late, they will have no flowers to rest in, which could reduce their life span and expose them to predation. This possible requirement of both fruit and flowers, then, limits the length of time that non-pollinators may exploit the mutualism.

The distribution of yucca plants in space may also determine which plants are exploited by non-pollinators. For example, an isolated plant may either be heavily hit by non-pollinators, because it is the only plant available to moths that find it, or it may be completely ignored because moths never find it. As well, there may be an interaction between how the distribution of yuccas in space and time affect exploitation by non-pollinators. A highly isolated yucca with flowers and fruit may be heavily hit by non-pollinators, since it is the only available yucca in which to mate and oviposit. An isolated yucca with fruit only, however, may be completely ignored, as the moths will have nowhere to mate, and will have to fly to other yuccas. By focusing non-pollinator activity on a few yuccas, the distribution of yuccas in space and time may limit the exploitation of some yuccas, and increase the impact on others.

Finally, in Chapter 5, I review the answers to these questions, and outline some possible future studies that stem from this project. Then, I conclude, by discussing the general role that each potential limit to exploitation plays in lowering exploitation, and therefore promoting coexistence between yuccas, their pollinators, and their exploiters.

Literature Cited

Addicott, J. F. 1996. Cheaters in yucca/moth mutualism. *Nature (London)* 380: 114-15.

Addicott, J. F. and A. J. Tyre. 1995. Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72: 382-94.

Addicott, J. F., Bronstein J. and Finn Kjellberg. 1990. Evolution of Mutualistic Life-Cycles: Yucca Moths and Fig Wasps. *Insect Life Cycles.* Editor Francis Gilbert, 143-61. London: Springer-Verlag.

Aker, C. L. and D. Udovic. 1981. Oviposition and pollination behaviour of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49: 96-101.

Alexander, R. D. and G. Borgia. 1978. Group selection, altruism, and the levels of organization of life. *Annual Review of Ecology and Systematics* 9: 449-74.

Alexandersson, R. and J. Agren. 1996. Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. *Oecologia* 107: 533-540.

Axelrod, R. and D. Dion. 1988. The further evolution of cooperation. *Science* 242: 1385-90.

Axelrod, R. and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211: 1390-1396.

Baker, H. G. 1986. Yuccas and yucca moths - a historical commentary. *Annals of the Missouri Botanical Gardens* 73: 556-64.

Bawa, K. S. 1980. Mimicry of male flowers by female flowers and intrasexual competition for pollinators in *Jaracharatia dolichaula* (D. Smith) Woodson (Cariceae). *Evolution* 34: 467-74.

Begon, M., Harper J. L. and C. R. Townsend. 1990. *Ecology: Individuals, Populations and Communities*. Boston, USA: Blackwell Scientific Publications.

Boyden, T. C. 1982. The pollination biology of *Calypso bulbosa* var. *americana* (Orchidaceae): Initial deception of bumblebee visitors. *Oecologia* 55: 178-84.

Connor, R. C. 1995. The benefits of mutualism: A conceptual framework. *Biology Reviews of the Cambridge Philosophical Society* 70, no. 3: 427-57.

Dafni, A. 1984. Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15: 259-78.

———. 1983. Pollination of *Orchis capsia* - a nectarless plant which deceives the pollinators of nectiferous species from other plant families. *Journal of Ecology* 71: 467-74.

———. 1983. Pollination of *Orchis capsia* - a nectarless plant which deceives the pollinators of nectiferous species from other plant families. *Journal of Ecology* 71: 467-74.

Dafni, A. and Y. Ivri. 1981. Floral mimicry between *Orchis israelitica* Baumann and Dafni (Orchidaceae) and *Bellevalia flexuosa* Boiss. (Liliaceae). *Oecologia* 49: 229-32.

Dodd, R. J. and Y.B. Linhart. 1994. Reproductive consequences of interactions between *Yucca glauca* (Agavaceae) and *Tegeticula yuccasella* (Lepidoptera) in Colorado. *American Journal of Botany* 81, no. 7: 815-25.

Doolitle, W. F. and C. Sapienza. 1980. Selfish genes, the phenotype paradigm, and genome evolution. *Natire* 284: 601-3.

Dugatkin, L. A. 1997. The evolution of cooperation: Four paths to the evolution and maintenance of cooperative behaviour. *BioScience* 47, no. 6: 355-62.

———. 1991. Tit for tat in guppies: the relative nature of cooperation and defection during predator inspection. *Evolutionary Ecology* 5: 300-309.

Enquist, M. and O. Leimar. 1993. The evolution of cooperation in mobile organisms. *Animal Behaviour* 45: 747-57.

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs* 48: 269-87.

———. 1983. Variable nectar secretion in a *Heliconia* species pollinated by Hermit hummingbirds. *Biotropica* 15: 48-52.

Ferriere, R. and R. E. Michod. 1996. The evolution of cooperation in spatially heterogeneous populations. *The American Naturalist* 147, no. 5: 692-717.

Fuller, O. S. 1990. "Factors affecting the balance of cooperation and conflict between the yucca moth, *Tegeticula yuccasella* and its mutualist, *Yucca glauca*." University of New Mexico.

Gorlick, D. L., Atkin P. D. and G. S. Losey. 1978. Cleaning stations as water holes, garbage dumps and sites for the evolution of reciprocal altruism. *The American Naturalist* 112: 341-43.

Hamilton, W. D. 1964. The genetical theory of social evolution I and II. *Journal of Theoretical Biology* 6: 1-52.

Hart, B. L. and L. A. Hart. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus. Animal Behaviour* 44: 1073-83.

Houston, A. I. 1993. Mobility limits cooperation. *Trends in Ecology and Evolution* 8: 194-96.

Inouye, D. W. 1983. The ecology of nectar robbing. *The Biology of Nectaries.* editors B. Bentley and T. Elias, 153-73. New York: Columbia University Press.

Inouye, D. W. 1980. The terminology of nectar larceny. *Ecology* 61, no. 5: 1251-53.

Janzen, D. H. 1975. *Pseudomyrex nigropilosa*: A parasite of a mutualism. *Science* 183: 936-37.

Jarvis, J. 1981. Eusociality in a mammal: cooperative breeding in the naked mole-rat. *Science* 212: 571-73.

Jarvis, J., O'Riain M. J., Bennett N. C. and P. W. Sherman. 1994. Mammalian eusociality: a familiy affair. *Trends in Ecology and Evolution* 9: 47-51.

Kerdelhue, C. and J. Rasplus. 1996. Non-pollinating Afrotropical fig wasps affect fig-pollinator mutualism in *Ficus* within the subgenus Sycomorus. *Oikos* 75: 3-14.

Kingsolver, R. W. 1983. Vegetative reproduction as a stabilizing feature of the population dynamics of *Yucca glauca. Oecologia* 69: 380-387.

Letourneau, D. K. 1990. Code of ant-plant mutualism broken by parasite. *Science* 248: 215-17.

———. 1991. Parasitism of ant-plant mutualisms and the novel case of *Piper*. *Ant-Plant Interactions* Chapter 25: 390-418.

Losey, G. C. 1972. The ecological importance of cleaning symbiosis. *Copeia* : 820-823.

Louda, M. 1982. Inflorescence spiders: A cost-benefit analysis for the host plant *Haplopappus venetus* Blake (Asreraceae). *Oecologia* 55: 185-91.

Mesterton-Gibbons, M. 1992. Cooperation among unrelated individuals: Evolutionary factors. *The Quarterly Review of Biology* 67, no. 3: 267-81.

Milinski. M. 1987. TIT FOR TAT in sticklebacks and the evolution of cooperation. *Nature* 325: 433-35.

Morris, W. F. 1996. Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology* 77, no. 5: 1451-62.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology* 31: 319-28.

Nowak, M. and K. Sigmund. 1993. Chaos and the evolution of cooperation. *Proceedings of the National Academy of Sciences, USA*. 90: 5091-94.

———. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* 364: 56-58.

Pellmyr, O., Leebens-Mack J. and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-56.

Prys-Jones, O. E. and Willmer P. G. 1992. The biology of alkaline nectar in the purple toothwort (*Lathraea clandestina*): ground level defenses. *Biological Journal of the Linnean Society* 45: 373-88.

Pyke, G. H. 1981. Optimal nectar production in a hummingbird pollinated plant. *Theoretical Population Biology* 20: 326-43.

Rettenmyer, C. W. 1970. Insect mimicry. *Annual Review of Entomology* 15: 43-74.

Ridley, M. 1993. *Evolution*. Hamilton, New York: Blackwell Scientific Publications, Inc.

Riley, C. V. 1892. The yucca moth and yucca pollination. *Annual Report of the Missouri Botanical Garden* 3: 99-159.

Rissing, S., Pollock G., Higgins M., Hagen R. and D. Smith. 1991. Foraging specialization without relatedness or dominance among co-founding ant queens. *Nature* 338: 420-422.

Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63, no. 2: 354-60.

Roubik, D. W., Holbrook N.M. and German Parra V. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161-67.

Soberon Mainero, J. and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic systems. *The Biology of Mutualism*. editor D. H. Boucher, 192-216. London: Croom Helm.

Stephenson, A.G. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *Journal of Chemical Ecology* 8, no. 7: 1025-34.

———. 1981. Toxic nectar deters nectar thieves of *Catalpa speciosa*. *The American Midland Naturalist* 105, no. 2: 381-83.

Thompson, J. N. 1982. *Interactions and Coevolution*. New York: John Wiley and Sons.

Trivers R.L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46, no. 35-57.

Turner, J. R. G. 1987. The evolutionary dynamics of Batesian and Muellerian mimicry: similarities and differences. *Ecological Entomology* 12: 81-95.

Turner, J. R. G., Kearney E. P. and L. S. Exton. 1984. Mimicry and the Monte Carlo predator: the palatability spectrum and the origins of mimicry. *Biological Journal of the Linnean Society* 23: 247-68.

Tyre, A. J. and J. F. Addicott. 1993. Facultative non-mutualistic behaviour by an "Obligate" mutualist: "Cheating" by Yucca moths. *Oecologia* 94: 173-75.

Udovic, D. 1981. Determinants of fruit set in *Yucca whipplei*: Reproductive expenditure vs. pollinator availability. *Oecologia* 48: 389-99.

Udovic, D. and C. L. Aker. 1981. Fruit abortion and the regulation of fruit number in *Yucca whipplei*. *Oecologia* 49: 245-48.

West, Stuart A. and Edward Allen Herre. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London B.* 258: 67-72.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308: 181-84.

Wilson, D. S. 1983. The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14: 159-87.

———. 1990. Weak altruism, strong group selection. *Oikos* 59, no. 1: 135-40.

Wilson, D. S. and E. Sober. 1994. Re-introducing group selection to the human behavioural sciences. *Behavioural and Brain Sciences* 17: 585-654.

Woolfenden, G. E. and J. W. Fitzpatrick. 1984. *The Florida Scrub Jay: Demography of a Cooperative Breeding Bird.* Princeton, New Jersey: Princeton University Press.

Chapter 2

The Role of Mutualists in Limiting Exploitation

Abstract

The obligate mutualism between pollinating yucca moths and yucca plants is exploited by a member of the yucca moth complex whose larvae depend solely on yucca seeds for nutrition, but whose adult moths provide no pollination service to the yucca. I examined the role of a yucca plant (*Yucca kanabensis)* and its pollinating yucca moths (*Tegeticula yuccasella* spp) in limiting exploitation by a non-pollinating yucca moth (*T. yuccasella* spp.). Specifically, I addressed whether yucca plants limit exploitation by non-pollinators through selective abscission of yucca fruit and whether pollinating yucca moths indirectly limit exploitation by decreasing non-pollinator survivorship through interspecific competition between the species of larvae in yucca fruit.

I found that the yuccas do not selectively abscise yucca fruit with high non-pollinator oviposition loads, as some species do with high numbers of pollinator oviposition loads. In fact, fruit with high numbers of non-pollinator ovipositions were more likely to be retained by the plant. This is because non-pollinators oviposit in fruit 8 days and older, after 92% of fruit that are abscised, are already dropped. I did, however, find strong evidence of interference competition between the larvae of pollinator moths and non-pollinator moths; survivorship and seed consumption of non-pollinators decreased dramatically as a function of increasing numbers of pollinators. I conclude, therefore, that yuccas do not play a role in limiting exploitation by the non-pollinator, but pollinating yucca moth larvae play a strong role.

Introduction

One of the most intriguing problems in ecology is how cooperation or mutualism has evolved among inherently selfish organisms (Axelrod and Hamilton 1981; Axelrod and Dion 1988,;Nowak and Sigmund 1993a and 1993b; Dugatkin 1997; Mesterton-Gibbons 1992; Connor 1995; Wilson 1980, 1983, 1990). There are at least five hypotheses for how mutualism could arise - kin selection, reciprocal altruism, evolution of avirulence, by-product mutualism, and group selection.

Two major challenges in understanding the evolution or persistence of mutualisms are cheating and exploitation (Axelrod and Hamilton 1981, Axelrod and Dion 1987, Soberon and Martinez 1985). Cheating and exploitation of mutualisms are similar processes that involve different individuals. Cheaters are members of mutualistic species that receive the benefits of mutualism, but do not reciprocate. Exploiters, on the other hand, are members of species that never participate in the mutualism they exploit, but benefit from it, often to the detriment of one or both mutualists (Soberon and Martinez 1985).

The exploitation of mutualisms is reasonably well documented, particularly in plant-pollinator interactions. Exploiters in these systems include nectar robbers which consume plant nectar, but do not pollinate (Roubik et al 1985, Morris 1996, Inouye 1980, Wyatt 1980), parasitic fig wasps that lay eggs in fig syconia, but do not pollinate the fig (Kerdelhue and Rasplus 1996, Bronstein 1991, West and Herre 1994), and mimetic plants that attract another plants' pollinators, but do not provide any nectar in exchange for pollination (Dafni 1984, Brown and Kodric-Brown 1979, Dafni and Ivri 1981).

Studies of the exploiters of plant-pollinator mutualisms have generally focused on two issues: 1) identifying and understanding the life-history of the exploiter (Bultman and Mathews 1996, Bronstein 1991, Kerdelhue and Rasplus 1996), and 2) determining the impact of the exploiter on one or both of the mutualists (Bultman and Mathews 1996, West and Herre 1994, Bronstein 1991, Roubik 1985, McDade and Kinsman 1980). These studies have shown that the degree to which exploiters depend on mutualists is highly variable. Some are facultative opportunists, such as nectar robbers, which parasitize the mutualisms between many different flowers and pollinators (Roubik et al 1985, Roubik 1982). Others obligately depend on the mutualism between just two partners, such as non-pollinating fig wasps (Bronstein 1991, West and Herre 1994). Further, the impact that exploiters have on mutualists ranges widely from little or no impact (Morris 1996) to severe (Roubik 1985).

If the exploiter has a severe negative impact on the fitness of mutualists, mutualists may be selected for traits that limit the exploitation. To limit the impact of nectar robbers, flowers often have thickened calyxes that are difficult to pierce (Inouye 1983), long fused corollas (Inouye 1983), and nectar with chemicals benign to pollinators, but toxic to exploiters (Stephenson 1981, Stephenson 1982, Prys-Jones 1992). These studies are among the few that have examined the role of the mutualists in limiting exploitation.

I set out to examine both the impact of exploitation, and the processes that limit exploitation in the yucca-yucca moth mutualism. In this system, yucca moths, (*Tegeticula yuccasella* spp.), actively gather yucca pollen with specialized mouth parts called maxillary tentacles. They then fly to a flower on another inflorescence, oviposit into the flower's ovary, and actively pollinate the flower (Riley 1892, reviewed in Addicott 1990, and Powell 1992). By pollinating, the moth improves the chances that the flower will be retained as fruit, and that her progeny, which feed solely on developing yucca seeds, will survive (Keeley 1986, Addicott 1986).

In some areas, this mutualism is exploited by a non-pollinating yucca moth. This moth also belongs to the *T. yuccasella* complex, but is 50% larger than the pollinating yucca moths, and because it has vestigial maxillary tentacles, it cannot carry pollen (Addicott 1990, Addicott 1996, Pellmyr et al. 1996). Moreover, it lays eggs directly in the seeds of yucca fruit that have already been pollinated, and therefore does not need to pollinate. As a result, this moth truly exploits the mutualism - it feeds on yucca seeds, and exploits the pollination service of the yucca moth.

Non-pollinating moths could have a devastating effect on the yucca-yucca moth mutualism. Addicott (1996) has found as many as 50 non-pollinating larvae in yucca fruit, far more than the 15-18 larvae required to destroy all of the larvae in a fruit (Addicott 1986). As well, Pellmyr et al. (1996) have found significantly greater seed losses in fruit with non-pollinator larvae, than fruit without. But despite the large, and potentially destabilizing effect of non-pollinators of the yucca-yucca moth mutualism, mutualists and non-pollinators appear to have coexisted for a long time (Pellmyr et al. 1996), suggesting that there are processes that limit the damage caused by the non-pollinating moth.

In this chapter I examine both the impact of exploitation on the yucca-yucca moth mutualism, and the role that the mutualists play in limiting that exploitation. First, I examine whether the yucca limits exploitation by selective abortion of fruit. In several yucca-yucca moth systems, yuccas appear to regulate cheating by pollinators through selective abscission of flowers with very high oviposition loads (Pellmyr and Huth 1994; Richter and Weiss 1995; Addicott 1998). I suggest that yuccas could also limit exploitation by non-pollinators through selective abscission of fruit with high non-pollinator oviposition loads. Second, I examine the role of pollinator larvae in limiting non-pollinator exploitation. I predict that pollinator larvae play a role through interspecific competition with non-pollinator larvae that lowers non-pollinator survival, weight and seed consumption.

Materials and Methods

Study Site and Study Organisms

I studied interactions between yucca moths (*Tegeticula yuccasella* spp.), yuccas (*Yucca kanabensis* (McKelvey)), and an unnamed non-pollinating yucca moth (*T. yuccasella* spp.) (Addicott 1996) at two sites from June 12 to July 24 1995, and May 18 to July 18 in 1996. The "Yellow Jacket" site is located near Yellow Jacket Ranch near Coral Pink Sand Dunes State Park, Utah, USA. The "Old 89" site is located on the north side of the old US 89 Highway between Mt. Carmel and Kanab, Utah, USA (see Addicott and Tyre 1995 for a detailed description of the study sites).

Impact of the Non-pollinator

I examined the impact of non-pollinators on seed production at the Old 89 observation site in 1996. I randomly collected 1-2 fruit from all plants on the site, 28 days after I first noticed evidence of non-pollinator oviposition (see below). I collected at this time in an effort to harvest fruit with mature fourth instar non-pollinators that had not yet exited the fruit. I dissected the fruit and counted the number of non-pollinator larvae per fruit, the number of pollinators per fruit, and the number of seeds that were either intact or destroyed per fruit. Some of the pollinator larvae began to exit the fruit before they were harvested, so I placed bags over the fruit that I intended to harvest, and counted the number of larvae that had left the fruit each morning. Then, I summed the number of larvae that emerged per fruit and the number of pollinators remaining in the fruit to get an estimate of the number of pollinators per fruit.

To analyze the data, I determined the average number of seeds destroyed per non-pollinator in fruit with different numbers of larvae. Then, I used the calculation of seeds destroyed per larva in fruit with different larval loads to calculate both the average number of seeds per fruit that were damaged by non-pollinators, and the distribution of the proportion of seeds destroyed by non-pollinators per fruit. I also calculated the proportion of yucca fruit with and without non-pollinator larvae, and determined the mean ± standard error of non-pollinators per fruit when they were present.

Limitation of Non-pollinators by Yuccas

a) Reliability of Droplets: When non-pollinators oviposit in yucca fruit, droplets form on the fruit. I compared the cumulative number of droplets observed on fruit over time to the number of non-pollinator oviposition scars in fruit to determine if droplets were reliable indicators of both the presence and number of ovipositions. To do this, I recorded the number of droplets on all fruit on all plants at the Yellow Jacket observation site daily from 10:00 to 19:00 from 4 to 24 July, 1995 (the entire non-pollinator flight season). On 3 August 1995, I randomly collected 1-2 fruit per plant, dissected them, and counted non-pollinator oviposition scars. I recorded non-pollinator oviposition scars by lifting the seeds out of a locule, and looking for small, elliptical marks on the inside of the locule wall that were accompanied by marks on adjacent seeds. In 1996 at the "Old 89" observation site, I followed the same procedure, and recorded droplets from 9 June to 3 July from 6:00 to 10:00 each day. By observing droplets early in the morning in 1996, I minimized the risk of droplets being eaten by insects or washed away by thunderstorms, which occurred in 1995. I used linear regression to determine the relationship between the cumulative number of droplets and the number of ovipositions per fruit. Droplets were reasonable qualitative indicators of non-pollinator oviposition activity, as the number of ovipositions increased with the number of droplets (1995:$r^2 = 0.26$, $p < 0.000$, d.f. = 71, F = 26.21; 1996: $r^2 = 0.39$, $p < 0.000$,d.f. = 245, F = 156.83). Therefore, I continued to use droplets throughout 1995 and 1996 as an indication of non-pollinator ovipositions on fruit.

b) Fruit abortion by Yuccas: I examined the role of non-pollinators in yucca fruit abortion at the 1995 Yellow Jacket observation site. During the flowering season, I recorded the date that each flower opened so that I would know how old the fruit were when non-pollinators oviposited in them. Then, I recorded the identity and presence of all fruit on all plants at the beginning of the non-pollinator flight season. During the season, I recorded the number of droplets on each fruit on the site (see above) and, 10 days after the season finished, I recorded the number and identity of the fruit that remained on the site.

To analyze these data, I used logistic regression to determine if fruit retention was affected by the cumulative number of droplets (and therefore the number of ovipositions) seen on the fruit. To determine if there was a difference in the age of fruit that did or did not have droplets on a given plant, I used an Analysis of Covariance. Here, I blocked by plant to remove between-plant variation in fruit age, because the fruit that non-pollinators choose to oviposit in may be influenced by the choices they have on a given plant. I also used date as a covariate, because the age of fruit increased each day.

c) Flower and Fruit Abortion: In 1996 on a small, 20-plant site on "Old 89", I recorded the age at which flowers and fruit were abscised to determine the risk of abortion that non-pollinators face by ovipositing in fruit of different ages. I identified individual flowers on the site by recording their axil and wave position on the inflorescence. Every day I recorded the date that each flower opened, and recorded the date that the flower began to enlarge and/or the date that it was abscised. To analyze these data, I determined the mean age of flower or fruit abscission, and found the cumulative probability that abscised flowers and fruit were aborted on a given day after flower opening.

Limitation of Non-pollinators by the Yucca Moth

a) Non-pollinator survival - I examined the effect of interspecific competition between yucca moth larvae and non-pollinator larvae in 1995 and 1996 on fruit from experimental plants, and fruit from observational plants. In 1995, I collected fruit from the "Yellow Jacket" site that were an average of 46 days old. I dissected the fruit, and recorded the number of non-pollinator oviposition scars, the number of yucca moth larvae, and the number of non-pollinator larvae in each fruit. In 1996, I used fruit from the "Old 89" 1996 observation site, but collected them 28 days after droplets were first seen on a given plant to standardize the age of nonpollinators at fruit harvest. I then recorded the number of non-pollinators, the number of non-pollinator oviposition scars and the number of yucca moth larvae per locule per fruit. I also counted the number of seeds per locule per fruit and determined the number that had been damaged by larvae.

In 1996, about 1 km from the Old 89 observation site, I performed an experiment to determine if interspecific competition affected non-pollinator larvae differently as they matured. I placed non-pollinators on yucca fruit in cages with moth-pollinated fruit of known age and allowed them to oviposit for one night. I then collected the fruit either 12 or 29 days after oviposition and recorded the number of non-pollinator oviposition scars, the number of non-pollinator larvae, the number of yucca moth larvae and the number of seeds remaining intact and destroyed.

To analyze the effect of competition on non-pollinator survival, I used logistic regression to compare the proportion of non-pollinator oviposition scars in a locule that were associated with non-pollinator larvae. For the 1995 data, I examined whether non-pollinator survival was affected by the number of yucca moth larvae per locule. For the 1996 data, I changed 2 aspects of the analysis. First, I looked at non-pollinator survival of 12 day old (first instar) and 28 day old (fourth instar) non-pollinator larvae separately, to determine if interspecific competition had a different affect on non-pollinator larvae of different ages. Second, I included the age of pollinator larvae on the date of non-pollinator oviposition into fruit in the 1996 analysis. I did this to determine if the age difference between non-pollinator and pollinator larvae significantly affected non-pollinator survival.

For this analysis, I used only locules with 1-5 non-pollinator ovipositions to eliminate a potentially confounding effect of intraspecific competition between non-pollinators. As well, I used the locule within a fruit as the sample unit since larvae were usually contained within a locule, except at high densities.

I attempted to determine if a decrease in non-pollinator survival was simply due to exploitation competition because pollinator larvae eat many of the seeds before non-pollinator larvae begin feeding, or due to interference competition in which pollinator larvae eat young pollinator eggs and larvae as they tunnel through yucca seeds. I compared survival of non-pollinators inside pollinator feeding tunnels, outside of feeding tunnels, in locules with no pollinators and a wide range of non-pollinator ovipositions, and in control locules with no pollinators and only 1-5 ovipositions per locule (to limit intraspecific competition). I determined the proportion of non-pollinator oviposition scars associated with non-pollinator larvae in each treatment, arcsine square root transformed the data, and analyzed the data with an ANOVA and post hoc Least Significant Difference (LSD) tests.

b) Non-pollinator weight and seed consumption - To determine the effect of pollinator larvae on non-pollinator weight, I weighed 28 day-old non-pollinator larvae that came from locules with different numbers of pollinators. I then analyzed the data with linear regression. To determine the effect of pollinators on non-pollinator seed consumption, I compared the number of seeds eaten in locules with different numbers of 28 day old fourth instar non-pollinator and pollinator larvae. For this analysis, I used non-linear regression, and fit an inverse function ($y = a + b(1/x)$) to the data, because I expected seed consumption to level off at high larvae densities.

Results

Impact of Non-pollinators

Non-pollinators consumed an average of 30.3% (±1%) of the seeds in yucca fruit, with a range from 0 to 74% (Figure 2.1). In 1995, at Yellow Jacket, 99% of fruit had at least one non-pollinator oviposition scar (85 out of 86), and only 9.3% of yucca fruit did not have non-pollinator larvae in them. In those fruit that did have non-pollinator larvae, there were an average of 6.62 ± 0.65 non-pollinator larvae. In 1996, 92% of fruit had at least one non-pollinator oviposition scar (353 out of 386), but 45% of fruit did not have non-pollinator larvae. Those fruit that did have non-pollinator larvae had an average of 5.12 ± 0.35 non-pollinator larvae. The 1995 "Yellow Jacket" site had both a significantly higher proportion of fruit with non-pollinator larvae ($Z = 6.69$, $t_{0.05, 2, \infty} = 1.96$, $p < 0.05$), and a significantly higher proportion of fruit with non-pollinator ovipositions ($Z = 2.95$, $t_{0.05, 2, \infty} = 1.96$, $p < 0.05$) than the 1996 "Old 89" site.

Limits by the Yucca: Fruit Abortion

Yuccas did not selectively abort fruit with higher numbers of droplets (Figure 2.2). In fact, it appeared that fruit with high numbers of droplets were more likely to be retained (Wald = 45.49, $p < 0.000$, $R = 0.21$, $n = 1885$).

Non-pollinators avoid very young fruit, and focus oviposition activity on fruit of "middle age". In 1995 and 1996, I saw droplets on fruit between 8 and 30 days old at roughly equal intensity, but never saw droplets on fruit younger than 8 days and older than 30 days. As well, in 1995 the ages of fruit with and without droplets were different ($p = 0.013$, d.f. = 89, $F = 10.82$, Table 2.1, $n = 1231$ fruit); fruit with droplets were older (18.09 ± 0.54 days) than those without droplets (17.32 ± 0.41 days)(Figure 2.3). Meanwhile, 92% of fruit are aborted before they are 8 days old (Figure 2.4), with an average abscission age of 5.84 ± 0.01 (1780 flowers on 20 plants).

Limits by the Yucca Moth: Interspecific Competition

In 1995 non-pollinator survival decreased as the number of yucca moth larvae per locule increased ($n = 307$ locules, $p < 0.000$, Wald $= 5.11$, $R = -0.080$; Figure 2.5). In 1996, when I examined the effect of interspecific competition on non-pollinators of different ages, I found that for 12 day old non-pollinators, the number of yucca moth larvae in a locule had a strong negative impact on survival ($p<0.019$, $W = 5.52$, $R = -0.10$, $n = 181$ locules; Figure 2.6), but the difference in non-pollinator and pollinator ages did not affect survival. For 29 day old pollinators, though, both the number of pollinators per locule, and the age difference between the larvae species had a strong effect on non-pollinator survivorship (Pollinators: $p = 0.0005$, Wald $= 12.02$, $R= -0.213$; Age of pollinators: $p = 0.008$, Wald $= 7.14$, $R = 149$; $n = 184$ locules; Figure 2.7). Interspecific competition decreased survival of 29 day old non-pollinators, survival increased with the age of the pollinators at oviposition.

Survival of non-pollinators was lower inside pollinator feeding tunnels than in any other locule category ($p < 0.0000$, $F = 54.95$, d.f. $= 3$; Figure 2.8). But survival was not significantly different between control locules with no pollinators and only 1-5 oviposition scars, locules with no pollinators but a wide range of non-pollinator oviposition scars, locules with pollinators, but outside of non-pollinator feeding tunnels.

Interspecific larval density lowered the number of seeds eaten per larva; as the number of larvae per locule increased, the number of seeds consumed per locule increased, but quickly leveled off ($p < 0.000$, $F = 443.22$ $r^2 = 0.48$, d.f. $= 527$; Figure 2.9). However, non-pollinator weight changed little, if at all, with the increasing number of pollinators in a locule ($p = 0.036$, $F = 4.54$, $r^2 = 0.047$, d.f. $= 96$; Figure 2.10).

Despite the apparent strong negative impact of pollinators on non-pollinator survival and seed consumption, non-pollinator moths do not appear to avoid ovipositing in fruit with higher numbers of pollinators. This occurred at both the fruit level (1995: $r^2 = 0.001$, $p = 0.67$, $F = 0.18$, d.f. = 121; 1996: $r^2 = 0.002$, $p = 0.37$, $F = 0.81$, d.f. = 385), and the locule level (1995: $r^2 = 0.001$, $p = 0.42$, $F = 0.64$, d.f. = 732; 1996: $r^2 = 0.000$, $p = 0.48$, $F = 0.48$, d.f. = 2298; Figure 2.11).

Discussion

In this chapter, I have explained the potential impact of non-pollinators on yucca seed production, and then examined the role that both the yucca and the yucca moth play in limiting exploitation by the non-pollinator. My results show that the impact of non-pollinators varies widely among fruit, from causing no seed damage, to destroying 74% of the seeds per fruit. Yuccas do not appear to play a strong role in limiting exploitation through fruit abortion, indeed, fruit that were aborted had few droplets. Yucca moths, on the other hand, play a strong role in limiting exploitation through severe intraspecific competition that decreases non-pollinator survival.

Impact of Non-pollinators

Non-pollinators consumed an average of 30.3 % of yucca seeds in 1996, a figure considerably lower than the impact of some nectar robbers (Roubik 1982; Roubik et. al. 1985), but higher than reported for other nectar robbers (Morris 1996). In comparison to seed predation by pollinating yucca moths in this and other yucca-yucca moth systems, non-pollinators appear to consume a slightly higher proportion of seeds per fruit than the pollinators that have been studied (Keeley et al. 1983; Addicott 1986). There is also greater variation in seed predation by non-pollinators than pollinators, as non-pollinator seed consumption ranged from 0-74%. However, the seed predation by non-pollinator larvae may not be as intense as that of one of the pollinator larvae in our study sites (personal observations), whose damage to seed production has not yet been quantified.

The impact of non-pollinators on seed production in yuccas is quite clear; however, the impact of non-pollinators on the recruitment of yucca seedlings into the population is not. If yucca recruitment is limited by the number of seeds available, then non-pollinators may have a significant negative impact on sexual reproduction in yuccas. However, if seedling establishment is instead limited by the number of "safe sites" for yucca seedlings to establish, and the number of seeds exceeds the number of safe sites, non-pollinators may have little impact on yucca populations at all (Andersen 1988, 1989).

Limits by Yuccas

One of the key processes limiting the exploitation of mutualists is the ability of mutualists to first recognize the exploiter and then either ostracize or punish the exploiter (Axelrod and Hamilton 1981; Axelrod and Dion 1987). In the yucca-yucca moth system, several species of yuccas appear to be able to recognize cheating behaviour in pollinating yucca moths, and subsequently punish them (Pellmyr and Huth 1994; Richter and Weiss 1995; Wilson and Addicott 1997). These plants selectively abscise flowers with high numbers of ovipositions, possibly by detecting damage done to the flowers by moth ovipositors. This puts selective pressure on moths to avoid laying too many eggs in one flower, and the result is that the mutualism is regulated, and evolutionarily stable (Pellmyr and Huth 1994).

There appears to be no recognition and regulation of non-pollinators by *Yucca kanabensis*, however. Fruit with high numbers of droplets (and therefore ovipositions) were not selectively aborted, in fact, these fruit were retained at a remarkably high rate. I do not believe that the plant is responsible for this pattern by preferentially retaining fruit that are used heavily by non-pollinators. Rather, it is more likely that non-pollinators are ovipositing in fruit that are less likely to be abscised. I have never seen non-pollinators oviposit in fruit less than 8 days old, and 92% of flowers and fruit that are abscised are dropped before they are 8 days old. Non-pollinators, therefore, are not subject to the same regulation that some species of pollinating yucca moth are, because they oviposit in older fruit.

There may be two reasons why non-pollinators do not oviposit in young fruit. First, there may have been strong selection against ovipositing in young fruit due to fruit abortion. It is possible that non-pollinators in this system are derived from yucca moths that emerged late in the flowering season (Pellmyr et al. 1996a). Late in the season, there are few flowers to either oviposit in or collect pollen from, so moths may have begun to lay eggs in fruit (Aker and Udovic 1981). If they did so, there would be very strong selection to oviposit in older fruit since nearly 100% of abscission occurs in fruit younger than 8 days old. This is particularly true of flowers that bloom late in the season; by the end of the season, the plant has often set most or all of the fruit that it has resources to support, and so abscises the rest of the flowers (Humphries and Addicott, unpublished). On the other hand, non-pollinators may have evolved in another yucca-yucca moth system, and arrived in this system preadapted to oviposit in older fruit (Pellmyr 1992, Pellmyr et. al. 1996a, Pellmyr et. al. 1996b).

Limits by Yucca Moths

I did not determine the impact of the non-pollinators on pollinator larvae, but I expect that the total impact is small. Pollinator larvae can be as much as 30 days older than non-pollinators, and have often left the fruit, or are about to leave, by the time non-pollinator eggs begin to hatch. As a result, pollinator larvae have a distinct temporal competitive advantage over non-pollinators, and while the potential for them to harm non-pollinators is large, the reverse is not true. I expect only non-pollinators to lower pollinator survival, seed consumption and weight when non-pollinator moths oviposit in very young fruit. If non-pollinators oviposit in very young fruit, then the age difference between the larvae is minimized, and larval competition will not be as asymmetrical in favour of the older pollinator larvae. If there is even a 15 day gap between the non-pollinator and pollinator larvae, most of the pollinator larvae will exit the fruit before non-pollinators eat enough seeds to interfere with pollinator consumption.

There have been many studies on inter- and intraspecific competition for mutualistic resources between mutualists (Reviewed in Addicott 1985; Manasse and Howe 1983; Addicott 1978; Feinsinger 1976; Kodric-Brown and Brown 1978; Roubik 1978), where the impact of the density of one or several mutualists on the density of another has been examined. However, there are few studies of the impact that competition by exploiters has on mutualists (but see McDade and Kinsmen 1980; Roubik 1982), and fewer still on the impact of competition from mutualists has on exploiters (but see Roubik 1982; Janzen 1975).

I found some evidence of exploitation competition between yucca moth larvae and non-pollinator larvae. While there was almost no effect of competition on non-pollinator weight, there was a strong effect of competition on the number of seeds eaten by larvae. One reason that competition explained little of the variation in larvae weight, but did explain the pattern of seed consumption is that as locules became more crowded, larvae eat a larger proportion of each seed (Addicott 1986). This would diminish any effect of competition on larval weight, and calls the validity of my results on seed consumption into question. When I determined "seed consumption" I did not take into account the proportion of seeds eaten, instead I used just the number of seeds damaged. Had I taken the proportion of seeds eaten into account, I would probably have seen a smaller effect of competition on seed consumption at lower densities, and a much stronger effect at higher densities.

While I found some evidence of exploitation competition, I found very strong evidence of interference competition. First, survival appeared to decrease markedly with an increase in pollinator larvae for both first and fourth instar non-pollinators. Second, when I made the distinction between non-pollinator survival inside and outside of pollinator feeding tunnels, I found that survival decreased by about 95% in feeding tunnels. This suggests that, in general, the decrease in non-pollinator survival is not simply a function of seed depletion by non-pollinators. Rather, it indicates that non-pollinator eggs and young larvae that are in the feeding path of a pollinating larvae, may be eaten or killed. I conclude, then, that both exploitation and interference competition play a role in limiting non-pollinator survival overall, but that interference competition plays a stronger, and more direct role.

While interspecific competition had a strong negative affect on non-pollinator survival in both years, there is some preliminary evidence to suggest that competition may have been stronger in 1996. In 1995 I studied interspecific competition at the

Yellow Jacket study site. Here, there is only one species of pollinating moth ("deeps"), which lay eggs deep inside yucca flower ovaries, and which are regulated by the yuccas through selective abscission (Tyre and Addicott 1993; Addicott and Tyre 1995; Addicott 1998; Wilson and Addicott 1998). In 1996, I did this study at the "Old 89" site, where there are two species of pollinators, "deeps", and "shallows". The "shallows" lay eggs on the surface of the ovary, and are not regulated by the yucca, perhaps because the yucca cannot detect the oviposition damage. As a result, a yucca fruit can have as many as 40 shallow larvae in a fruit (personal observation), but only up to 15 or so deep larvae (Addicott 1986). Because there are greater numbers of pollinator larvae at the Old 89 site, interspecific competition might be much more severe at this site. Since interspecific competition reduces non-pollinator survival, this may explain two things: 1) why there were fewer fruit with non-pollinator larvae at Old 89 in 1996, than at Yellow Jacket in 1995, and 2) why the average number of non-pollinators per fruit that did have non-pollinators was lower at Old 89 than at Yellow Jacket. This is an interesting possibility; however, the number of fruit without non-pollinator oviposition scars also was higher at "Old 89", and the average number of ovipositions per fruit was also lower at "Old 89" (Chapter 3).

By using two different observation sites in the two years, it is more difficult to make comparisons about the level of oviposition activity between years, or the level of competition between years. However, the differences in the data at the two different sites do raise some interesting questions. It is possible that the severe competition faced by non-pollinators along Old 89 might eventually exclude them from this area, and either confine them to areas where *Yucca kanabensis* has only deep pollinators, or even force a host shift of non-pollinators onto co-occurring yuccas such as *Yucca baccata* or *Yucca utahensis*. Feder et al. (1995) suggested a similar interspecific competition-mediated host shift in the apple maggot fly from its preferred host, the hawthorn, to apples. As well, other scientists have suggested that natural selection for the use of host plants may be based partly on 'enemy-free space' (Thompson 1988; Price et al. 1980; Pierce and Elgar 1985; Price et al. 1986; Singer 1972).

Literature Cited

Addicott, J. F. 1978. Competition for mutualists: Aphids and ants. *Canadian Journal of Zoology* 56: 2093-96.

———. 1985. Competition in mutualistic systems. *The Biology of Mutualism.* editor D. H. Boucher, 217-47. London: Croom Helm.

———. 1986. Variation in the costs and benefits of mutualism: The interaction between yuccas and yucca moths. *Oecologia* 70: 486-494.

———. 1996. Cheaters in yucca/moth mutualism. *Nature (London)* 380: 114-15.

Addicott, J. F. and A. J. Tyre. 1995. Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72: 382-94.

Addicott, J. F., J. Bronstein, and F. Kjellberg. 1990. Evolution of Mutualistic Life-Cycles: Yucca Moths and Fig Wasps. *Insect Life Cycles.* 1 ed., Editor Francis Gilbert, 143-61. London: Springer-Verlag.

Aker, C. L. and D. Udovic. 1981. Oviposition and pollination behaviour of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49: 96-101.

Andersen, A. N. 1988. Insect predators may cause far greater losses than they appear to. *Oikos* 52, no. 3: 337-40.

———. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials. *Oecologia* 81: 310-315.

Axelrod, R. and D. Dion. 1988. The further evolution of cooperation. *Science* 242: 1385-90.

Axelrod, R. and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211: 1390-1396.

Bronstein, J. L. 1991. The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? *Oikos* 61: 175-86.

Brown, J. H. and A. Kodric-Brown. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* 60, no. 5: 1022-35.

Bultman, T. L. and P. L. Mathews. 1996. Mycophagy by a millipede and its possible impact on an insect-fungus mutualism. *Oikos* 75, no. 67: 74.

Connor, R. C. 1995. The benefits of mutualism: A conceptual framework. *Biology Reviews of the Cambridge Philosophical Society*

Dafni, A. 1983. Pollination of *Orchis capsia* - a nectarless plant which deceives the pollinators of nectiferous species from other plant families. *Journal of Ecology* 71: 467-74.

———. 1984. Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15: 259-78.

Dafni, A. and Y. Ivri. 1981. Floral mimicry between *Orchis israelitica* Baumann and Dafni (Orchidaceae) and *Bellevalia flexuosa* Boiss. (Liliaceae). *Oecologia* 49: 229-32.

Dugatkin, L. A. 1997. The evolution of cooperation: Four paths to the evolution and maintenance of cooperative behaviour. *BioScience* 47, no. 6: 355-62.

Feder, J. L. Reynolds K. Go W. and E. C. Wang. 1995. Intra- and interspecific competition and host race formation in the apple maggot fly, *Rhagoletis pomonella* (Diptera:Tephritidae). *Oecologia* 101: 416-25.

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs* 48: 269-87.

Inouye, D. W. 1980. The terminology of nectar larceny. *Ecology* 61, no. 5: 1251-53.

———. 1983. The ecology of nectar robbing. *The Biology of Nectaries.* editors B. Bentley and T. Elias, 153-73. New York: Columbia University Press.

Janzen, D. H. 1975. *Pseudomyrex nigropilosa*: A parasite of a mutualism. *Science* 183: 936-37.

Keeley, J. E., C. Sterling, and D. A Ikeda. 1986. Seed predation by yucca moths on semeparous, iteroparous and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). *The American Midland Naturalist* 115, no. 1: 1-9.

Kerdelhue, C. and J-Y Rasplus. 1996. Non-pollinating Afrotropical fig wasps affect fig-pollinator mutualism in *Ficus* within the subgenus Sycomorus. *Oikos* 75: 3-14.

Kodric-Brown, A. and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology* 59: 285-96.

Manasse, R. S. and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: Influences of neighbours. *Oecologia* 59: 185-90.

McDade, L. A. and S. Kinsman. 1980. The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. *Evolution* 34: 944-58.

Mesterton-Gibbons, M. 1992. Cooperation among unrelated individuals: Evolutionary factors. *The Quarterly Review of Biology* 67, no. 3: 267-81.

Morris, W. F. 1996. Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology* 77, no. 5: 1451-62.

Nowak, M. and K. Sigmund. 1993. Chaos and the evolution of cooperation. *Proceedings of the National Academy of Sciences, USA*. 90: 5091-94.

———. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* 364: 56-58.

Pellmyr, O. 1992. The phylogeny of a mutualism: evolution and coadaptation between *Trollius* and its seed-parasitic pollinators. *Biological Journal of the Linnean Society* 47: 337-65.

Pellmyr, O. and C. J. Huth. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature (London)* 372: 257-60.

Pellmyr, O., J. Leebens-Mack, and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-56.

Pellmyr, O., J.N. Thompson, J.M. Brown, and R. G. Harrison. 1996. Evolution of pollination and mutualism in the yucca moth lineage. *The American Naturalist* 148, no. 5: 827-47.

Pierce, N. E. and M. A. Elgar. 1985. The influence of ants on host plant selection by *Jalmenus exagoras*, a myrmecophilus lycaenid butterfly. *Behavioural Ecology and Sociobiology* 16: 209-22.

Powell, J. A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7, no. 1: 10-14.

Price, P. W., C.E. Boulton, P. Gross, B.A. McPherson, J.N. Thompson, and A.E. Weiss 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11: 41-65.

Price, P. W., M. Westoby, B. Rice, P.R. Atsatt, R.S. Fritz, J.N. Thompson and K. Mobly. 1986. Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics* 17: 487-505.

Prys-Jones, O. E. and Willmer P. G. 1992. The biology of alkaline nectar in the purple toothwort (*Lathraea clandestina*): ground level defenses. *Biological Journal of the Linnean Society* 45: 373-88.

Richter, K. S. and A. E. Weiss. 1995. Differential abortion in the yucca. *Nature (London)* 376: 557-58.

Riley, C. V. 1892. The yucca moth and yucca pollination. *Annual Report of the Missouri Botanical Garden* 3: 99-159.

Roubik, D. W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201: 1030-1032.

———. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63, no. 2: 354-60.

Roubik, D. W., N. Holbrook, V. German Parra 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161-67.

Singer, M. C. 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176: 75-77.

Soberon Mainero, J. and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic systems. *The Biology of Mutualism.* editor D. H. Boucher, 192-216. London: Croom Helm.

Stephenson, A. G. 1981. Toxic nectar deters nectar thieves of *Catalpa speciosa*. *The American Midland Naturalist* 105, no. 2: 381-83.

———. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *Journal of Chemical Ecology* 8, no. 7: 1025-34.

Thompson, J. N. 1983. Selection pressures on phytophagous insects feeding on small host plants. *Selection Pressures on Phytophagous Insects Feeding on Small Host Plants.* 40: 438-44.

Tyre, A. J. and J. F. Addicott. 1993. Facultative non-mutualistic behaviour by an "Obligate" mutualist: "Cheating" by yucca moths. *Oecologia* 94: 173-75.

West, S. A. and E. A. Herre. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London B.* 258: 67-72.

Wilson, D. S. 1980. *The natural selection of populations and communities.* Menlo Park, California: Benjamin Cummings.

———. 1983. The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14: 159-87.

———. 1990. Weak altruism, strong group selection. *Oikos* 59, no. 1: 135-40.

Wyatt, R. 1980. The impact of nectar-robbing ants on the pollination system of *Asclepias curassavica*. *Bulletin of the Torrey Botanical Club* 107, no. 1: 24-28.

Table 2.1: Analysis of Covariance to determine if the age of fruit with droplets was different than the age of fruit without droplets.

		SS	d.f.	MS	F	p
Covariate	Date	1140.8	1	1140.8	658.0	< 0.000
Main Effects	Plant	4910.9	87	56.4	32.6	< 0.000
	Droplets	10.8	1	10.8	6.2	0.013
Model		6192.2	89	69.6	40.132	<0.000
Residual		325.9	188	1.7		
Total		6518.2	277	23.5		

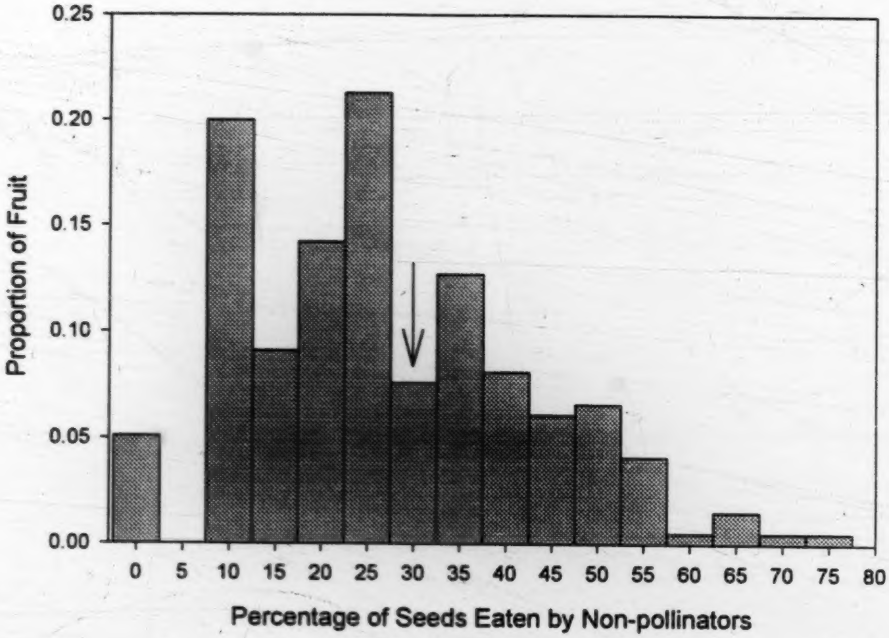

Figure 2.1: The proportion of yucca fruit with a given percentage of their seeds destroyed by non-pollinators in 1996. Mean seed consumption per fruit by non-pollinator larvae was 30.3%.

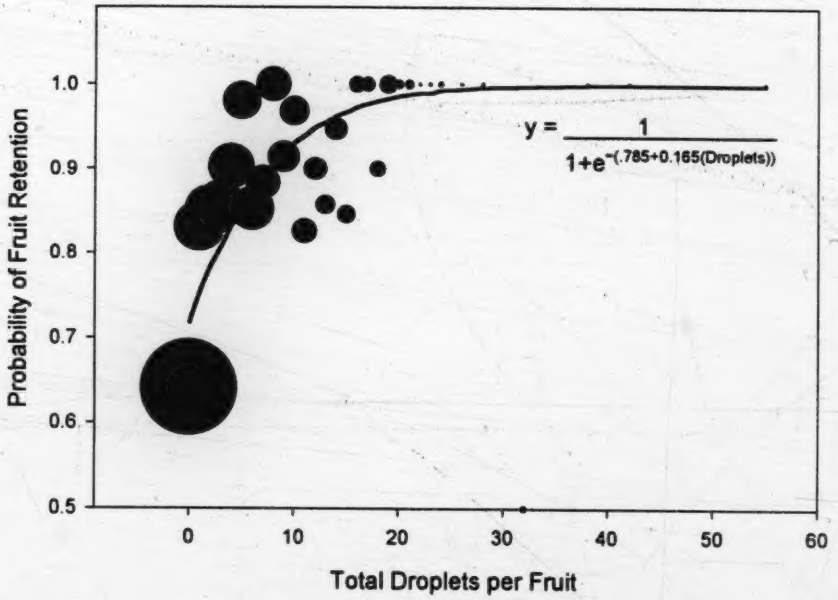

Figure 2.2: The probability that a fruit was retained as a function of the cumulative number of droplets it received. Bubble size is proportional to sample size.

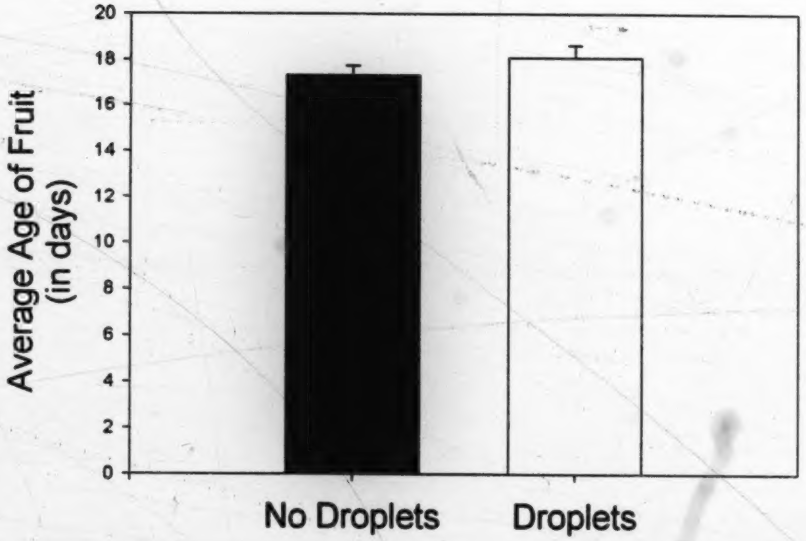

Figure 2.3: The average age of fruit with droplets and without droplets in 1995.

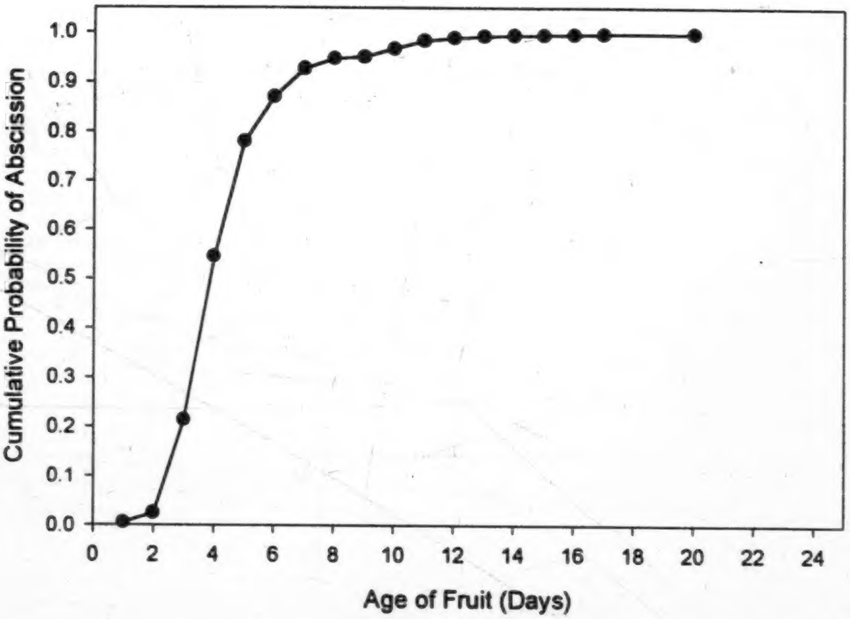

Figure 2.4: The cumulative probability that a fruit that is abscised will be dropped by a given age.

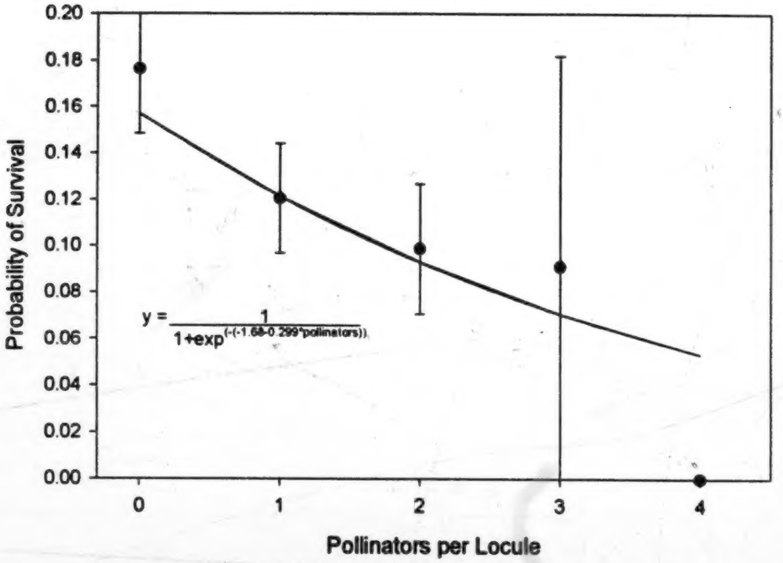

Figure 2.5: Probability of survival of non-pollinators (in locules with 1-5 oviposition scars) as a function of the number of pollinators per locule in 1995. Symbols represent the average probability of survival +/- standard error for locules with given numbers of pollinator larvae, and the line represents the probability of survival predicted by logistic regression.

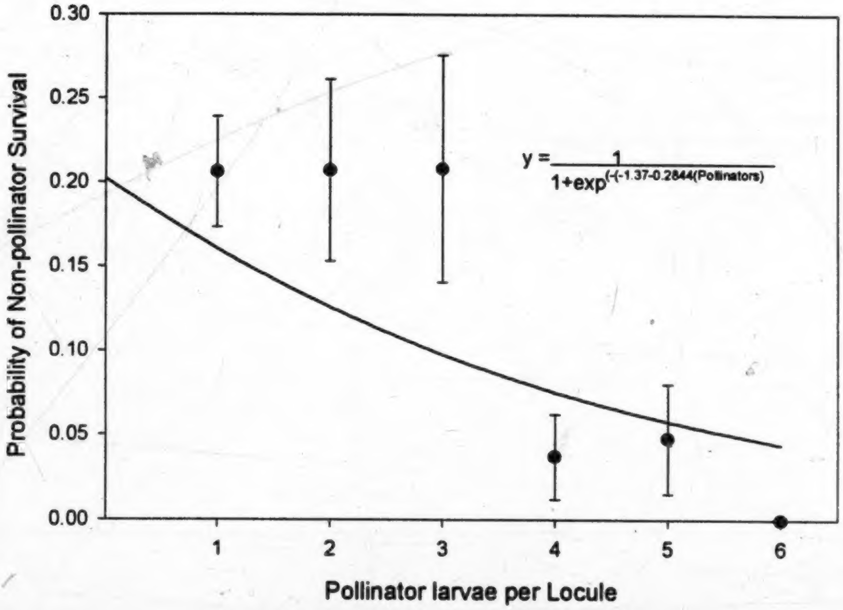

Figure 2.6: Probability that a non-pollinator oviposition scar will be associated with a larvae as a function of the number of pollinator larvae per locule for 12 day old non-pollinators in 1996. Shown here is the survival predicted by logistic regression (line), and the average survival in locules with different numbers of pollinators +/- standard error.

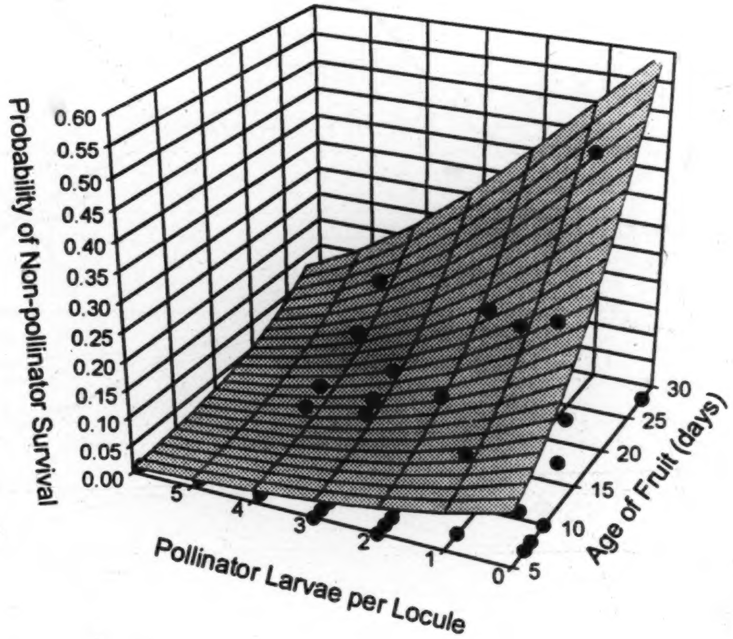

Figure 2.7: Probability of non-pollinator survival as a function of the number of pollinator larvae per locule, and the age of the fruit at non-pollinator oviposition for 28 day old non-pollinator larvae in 1996. Surface plot represents the survival predicted by a logistic regression; symbols represent average survival in a locule. $y = 1/1+\exp^{(-(2.89+(0.12*\text{Fruit Age}) - (0.40*\text{Pollinators})}$.

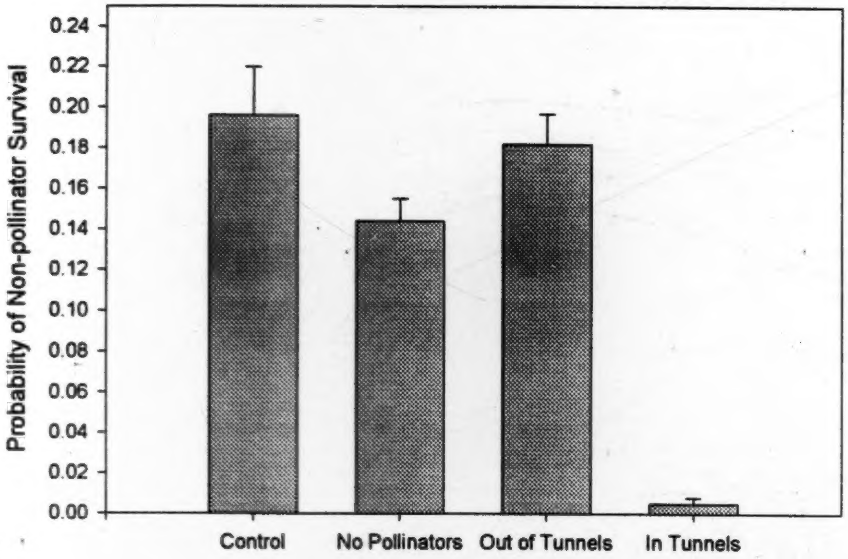

Figure 2.8: Probability of non-pollinator survival in control locules (no pollinators, 1-5 non-pollinator ovipositions, n = 150 locules), in locules with pollinators (n = 300), inside pollinator feeding tunnels (n = 433), and outside pollinator feeding tunnels (n = 433).

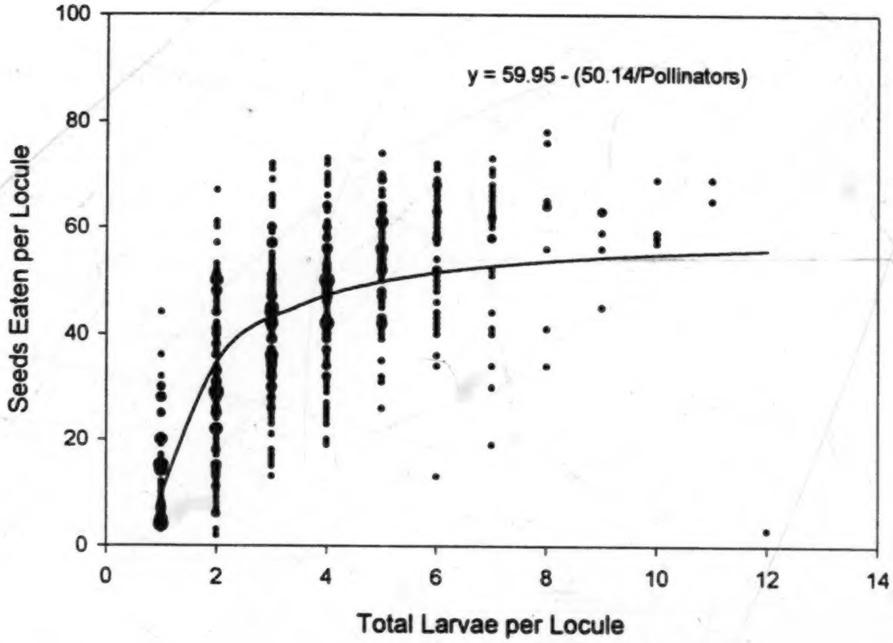

Figure 2.9: Seeds eaten per locule as a function of the number of larvae per locule.

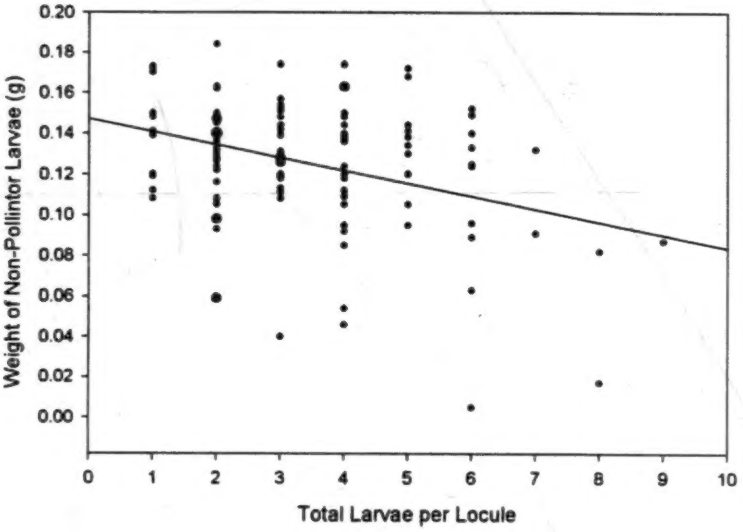

Figure 2.10. The weight of fourth instar larvae as a function of the number of fourth instar pollinator and non-pollinator larvae per locule.

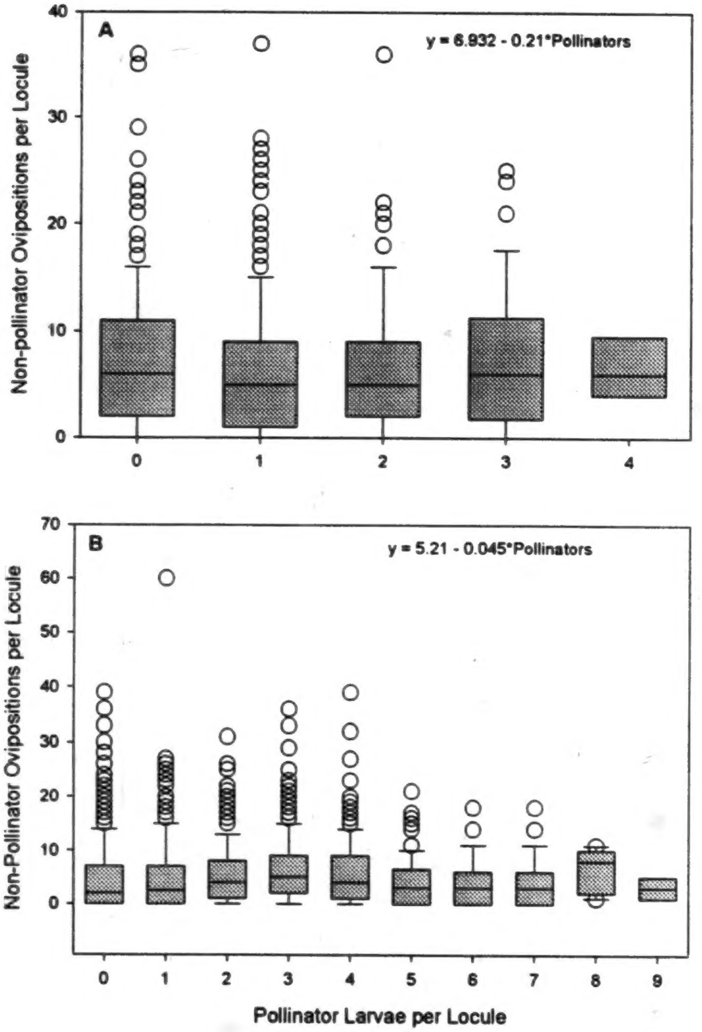

Figure 2.11: Non-pollinator ovipositions per locule as a function of the number of pollinator larvae per locule A) 1995 B) 1996.

Chapter 3

Intraspecific Competition and Non-pollinator Oviposition Patterns

Abstract

The recent interest in the three-way interactions between mutualists and the organisms that exploit them has generated many studies on the impact of exploiters on mutualists. A natural extension of these studies is to determine the factors that promote or limit exploitation of mutualisms. I examined the role of intraspecific competition between exploiters in regulating exploitation of the mutualism between the yucca plant, *Yucca kanabensis*, and its pollinator *Tegeticula yuccasella*, by a non-pollinating, seed-parasitic moth. Specifically, I examined the distribution of non-pollinator ovipositions in yucca fruit, to determine if there was potential for intraspecific competition between non-pollinator larvae in yucca fruit. Then, I determined if intraspecific competition affected non-pollinator survival, seed consumption, and weight, and determined at what instar stage intraspecific competition became noticeable.

I found that non-pollinator ovipositions were highly aggregated, and as a result, there was strong potential for intraspecific competition. However, I found only a modest affect of intraspecific competition on non-pollinator survival and seed consumption, and virtually no affect on weight. As well, intraspecific competition did not noticeably affect non-pollinator survival until the larvae reached fourth instar. This is explained by their patterns of feeding and movement, as non-pollinators eat very few seeds, and are immobile until fourth instar, so probably do not interfere with each other until this developmental stage.

Introduction

Recently, there has been great interest in studying the three-way interactions between mutualists and the organisms that exploit them (eg. Morris 1996; Bultman 1995; Bultman and Mathews 1996; Kerdelhue and Rasplus 1996; West and Herre 1994). Two kinds of organisms exploit mutualisms: 1) "cheaters" which are members of mutualistic species that receive benefit from the mutualism, but do not reciprocate; and 2) "exploiters" which are not members of the mutualistic species that they exploit, but who also benefit from the mutualism without providing benefit in return (Soberon and Martinez 1985). Studies of the interactions between cheaters and mutualists have focused on how cheating arises, how often it occurs, and how it is limited (Addicott and Tyre 1995; Tyre and Addicott 1993; Houston 1993; Fierrere and Michod 1996; Axelrod and Dion 1988). Studies of the interactions between mutualists and their exploiters, on the other hand, are not as well documented. Most studies focus solely on the impact of exploiters on mutualists (Roubik 1982; Roubik et. al. 1985; Morris 1996), but do not address either how exploitation arises, or how it is limited once it does arise (but see Pellmyr et al. 1996).

There may be several processes that limit the exploitation of mutualisms. In Chapter 2, I discussed the role of mutualists in limiting exploitation, and found that interspecific competition between the mutualist and the exploiter for mutualistic resources may play a strong role. In this chapter, I suggest that the exploiter itself may play a role in limiting exploitation through density-dependent intraspecific competition for mutualistic resources.

The role of intraspecific competition in limiting populations often depends on the life history and feeding strategies of organisms (Averill and Prokopy 1987, Thompson 1983, Roitberg and Prokopy 1987). In insects, for example, competition is expected to be stronger among those that feed in small, ephemeral, spatially restricted plant parts (such as flowers or fruit) than among those that "graze" upon the foliage of larger plants (Averill and Prokopy 1987, Thompson 1983, Roitberg and Prokopy 1987, Shorrocks 1990). This is because in spatially restricted patches, they have no option of moving away and exploiting alternative resources if crowding occurs. Support for these ideas comes from studies which demonstrate that competition lowers survival of fruit fly larvae in hawthorn fruit (Averill and Prokopy 1987, Feder et al. 1995), of stem borers in marsh grasses (Stiling and Strong 1983) and of cowpea seed beetle larvae in legume seeds (Credland et al. 1986, Smith and Lessells 1985)

In systems where intraspecific competition between larvae is likely to be high, there is strong selection for insects to avoid competition (Roitberg and Prokopy 1987, Averill and Prokopy 1987, Thompson 1983, Shapiro 1981). One way insects can limit competition in small plant parts is if females oviposit uniformly among patches (Shapiro 1981). A second way is for insects to evolve the ability to assess egg loads in a patch (Thompson 1983, Roitberg and Prokopy 1987, Averill and Prokopy 1987). Some species assess egg loads visually (Shapiro 1981, Messina 1985). For example, female pierid butterflies lay large, visible eggs which can be detected and avoided by other females. Other species assess egg loads chemically, by using pheromones to mark their hosts to deter conspecifics (Prokopy 1972, Prokopy et al. 1978). Often this is used by insects whose eggs are inconspicuous, such as the eggs of flies who oviposit in fruit.

In systems where insects lay eggs in fruit, the oviposition patterns of the adults determines the number of offspring in fruit, which in turn determines both the strength of competition between the larvae, and the extent to which fruit are exploited. For example, insects with highly aggregated distributions of ovipositions and larvae might experience severe intraspecific competition that would strongly regulate populations. On the other hand, insects with uniform oviposition patterns should not experience intraspecific competition until adult densities are very high. This lack of density-dependent population regulation would result in a greater total impact on fruit and seed production.

Many insects that oviposit in fruit can be considered to be exploiters, or parasites, of the mutualism between plants and their pollinators (Soberon and Martinez 1985). Their offspring exploit the plant by feeding on seeds and other plant tissues, and exploit the pollinator because fruit would not develop without pollination. Fruit are small, spatially restricted, ephemeral plant parts in which competition between exploiters is expected to be high, and in this kind of environment, regulation of exploitation through intraspecific competition is most likely to occur.

In the yucca-yucca moth system, yucca moths, *Tegeticula yuccasella* spp., actively gather yucca pollen with specialized mouth parts called maxillary tentacles. They then fly to a flower on another inflorescence, oviposit into the flower's ovary, and actively pollinate the flower (Riley 1892, reviewed in Addicott 1990, and Powell 1992). By pollinating, the moth improves the chances that the flower will be retained as fruit, and that her progeny, which feed solely on developing yucca seeds, will survive (Keeley 1984, Addicott 1986).

In some areas, this mutualism is exploited by a non-pollinating moth. This moth is derived from yucca moths, but is 50% larger than pollinating yucca moths, and because it has vestigial maxillary tentacles, it cannot carry pollen (Addicott et. al. 1990, Addicott 1996, Pellmyr et al. 1996). Like pollinating yucca moths, the larvae of non-pollinators feed solely on maturing yucca seeds. But unlike pollinators, non-pollinators lay eggs directly inside the seeds of yucca *fruit*, rather than ovipositing in the ovary of yucca flowers, and therefore need not pollinate. As a result, this moth truly exploits the mutualism - it exploits the seeds of the yucca, and the pollination service of the yucca moth.

The non-pollinating moth could have a devastating effect on the yucca-yucca moth mutualism. Addicott (1996) has found as many as 50 non-pollinating larvae in yucca fruit, far more than the 15-18 larvae required to destroy all of the larvae in a fruit. As well, Pellmyr et al. (1996) have found significantly greater seed losses in fruit with non-pollinator larvae, than fruit without. But despite the large, and potentially destabilizing effect of non-pollinators of the yucca-yucca moth mutualism, the mutualists and non-pollinator have coexisted for a long time (Pellmyr et al. 1996), suggesting that there are processes that limit the damage caused by the non-pollinating moth.

I suggest that density-dependent intraspecific competition between non-pollinator larvae may limit exploitation of the yucca-yucca moth mutualism by this moth. Yucca fruit are relatively small, ephemeral, spatially restricted food resources. As such, non-pollinator larvae could experience strong intraspecific competition, which in turn could regulate non-pollinator population sizes and limit the exploitation of the mutualism. Conversely, intraspecific competition may not play a strong role in regulation if non-pollinating moths oviposit uniformly by assessing egg loads in fruit (using droplets as a cue), and avoiding those that have been previously hit.

In this chapter, I examine the pattern of non-pollinator oviposition patterns in yucca fruit to determine 1) the potential for intraspecific competition between non-pollinator larvae in fruit, and 2) whether non-pollinating moths are capable of assessing egg loads in fruit, and therefore ovipositing uniformly, and decreasing the potential for intraspecific competition in fruit. Then, given the pattern of ovipositions, I examine the role of intraspecific competition between non-pollinators in regulating non-pollinator numbers, and limiting the exploitation of the yucca-yucca moth mutualism. In particular, I examine 1) the effect of competition on the survival of larvae in different instars, and on the seed consumption and weight of fourth instar larvae, and 2) the extent to which competition occurs in unmanipulated observation plants.

Materials and Methods

Study Site and Study Organisms

In this study, the "pollinators" are 2 species of *Tegeticula yuccasella* spp. that pollinate *Yucca kanabensis* (McKelvey). These mutualists are exploited by an unnamed non-pollinating moth, also of the *T. yuccasella* complex (Addicott 1996). In 1995, I performed observations and fruit collections from June 12 to July 24, at the "Yellow Jacket" site, located near Yellow Jacket Ranch near Coral Pink Sand Dunes State Park, Utah, USA. In 1996, I performed almost the same set of studies from 18 May to 18 July at the "Old 89" site, located on the north side of the old US 89 Highway between Mt. Carmel and Kanab, Utah, USA (for more details, see Addicott and Tyre 1995).

Non-Pollinator Oviposition Patterns

Droplets on Fruit over Time: In both 1995 and 1996, I recorded the number of droplets seen on every fruit within an observation site, each morning during the non-pollinator flight season. I then determined the number of times a fruit was seen with droplets in both the 1995 and 1996 flight seasons. I compared the pattern of the number of times a fruit was seen with droplets to a Poisson distribution, using a Kolmogorov-Smirnov test (Zar 1984).

Number of Droplets on Fruit: I used the information on the number of droplets on fruit seen on each morning (see above) to examine the pattern of the non-pollinator ovipositions on a per-night basis. For three days during the peak 1996 non-pollinator flight season, I determined the pattern of droplets on all fruit on the site, and then determined the pattern of droplets only on fruit that were on plants with at least one droplet. Then, I compared the pattern of droplets in each instance to a Poisson distribution using a Kolmogorov-Smironov test, and then used a negative binomial (Pielou 1969) to describe the pattern of ovipositions quantitatively.

Non-pollinator Oviposition Scars in Fruit and Locules: In both 1995 and 1996, I randomly collected 1-2 fruit per plant within the "Yellow Jacket" and "Old 89" observation sites and dissected them to determine the pattern of non-pollinator oviposition scars within fruit. I compared this pattern to a Poisson distribution using a Kolmogorov-Smirnov test, and then used a negative binomial (Pielou 1969) to describe the pattern of ovipositions. I repeated this process using the same fruit, but examining the pattern of non-pollinator oviposition scars on a locule level, rather than a fruit level.

Non-pollinator Larvae in Fruit and Locules: In the same fruit collected in 1995 and 1996 (see above), I also recorded the number of non-pollinator larvae per fruit, and per locule.

I compared the pattern of non-pollinator larvae within fruit to a Poisson distribution using a Kolmogorov-Smirnov test, and used a negative binomial to describe the pattern of larvae. I then repeated this pattern at the locule level.

Non-pollinator Oviposition Choice

In 1996 I performed an experiment to determine if non-pollinator oviposition choices are affected by whether a fruit has been previously oviposited in by another non-pollinator. First, I caged yucca plants while they were flowering and hand-pollinated the flowers, so that the fruit contained no pollinator larvae. Then, during the non-pollinator flight season, I collected moths (see below) and placed them in cages on the yucca plants in three different ways. For the control, I placed a non-pollinator in the bottom of the cage, and allowed it to oviposit in all fruit on the plant (4 or 6 fruit) on night 1. The next day, I counted the number of droplets on each fruit, and replaced the moth in the cage. On night 2, the fresh moth also chose between all of the fruit. In addition to the control, I had two treatments to eliminate the possibility that moths prefer to oviposit in fruit on either the top or the bottom of the inflorescence (bag effects). In Treatment 1, I allowed the moths to oviposit in fruit on the bottom inflorescence on Night 1. I counted the droplets the next morning, replaced the moth, and let the new moth choose between all of the fruit ("hit" and "unhit") on Night 2. In Treatment 2, the moth oviposited on top fruit on Night 1, and the new moth was allowed to choose between all fruit on Night 2. I compared the number of droplets on top or bottom fruit on Night 2 using an ANOVA because the replication was too low to perform a Kruskal-Wallis test.

Intraspecific Competition

Larval Survival

I examined intraspecific competition between non-pollinator larvae in both 1995 and 1996 in "experimental" and "observation" fruit. For "experimental" fruit, I placed window screen cages over yuccas before they began flowering to eliminate pollinators, and to prevent outside non-pollinators from laying eggs in fruit. I recorded the day a flower opened, and hand-pollinated fresh flowers. Then, during the non-pollinator flight season, I collected non-pollinators by gathering flowers containing female and/or male moths, and placing the flower and moths in a cooler. Once I collected the moths, I placed at least one male and one female (but as many as six females) in the bottom of the cages covering the yucca plants. I allowed the moths to oviposit in fruit for one night, and then removed them to keep the age of the larvae constant. In 1995, I collected and dissected fruit 8, 12, 18, 25 and 32 days after non-pollinators had been allowed to oviposit. These ages correspond roughly to eggs, first, second, third, and fourth instar larvae, respectively. In 1996 I followed the same procedure, but collected and dissected fruit with 12 day old and 29 day old larvae (first and fourth instar). While dissecting all fruit, I counted the number of non-pollinator oviposition scars and larvae in each of the six locules in a fruit. In these experiments, locules were considered the unit of observation, since larvae rarely crossed from one locule into another.

I also examined intraspecific competition in "observation fruit". In 1995, I randomly collected fruit from plants that still had fruit at the end of the non-pollinator flight season at the Yellow Jacket observation site. I dissected the fruit, and recorded the number of non-pollinator oviposition scars, yucca moth larvae, and non-pollinator larvae in each locule. In 1996, I randomly collected 1-2 fruit per plant from the Old 89 observation site, but collected them 28 days after I first saw droplets on a plant to standardize the age of non-pollinators at fruit harvest. I dissected the fruit as above, and analyzed the locules that only contained non-pollinators.

I used logistic regression to compare the proportions of non-pollinator oviposition scars in a locule associated with a non-pollinator larvae, as a function of ovipositions per locule and the age of non-pollinator larvae (in experimental fruit). In the 1996 experimental fruit, I also examined the effect of fruit age on non-pollinator survival to serve as a control for the interspecific competition experiment in which I examined the effect of the age of pollinator larvae on non-pollinator survival (see Chapter 2).

Non-pollinator Seed Consumption and Weight

While dissecting fruit (see above), I determined the number of seeds destroyed per locule by fourth instar non-pollinators in locules. As well, I determined the weight of fourth instar non-pollinators in locules with varying numbers of fourth instar non-pollinators. I analyzed both with linear regression.

Results

Non-pollinator Oviposition Patterns

The pattern of droplets on fruit all plants differed significantly from a Poisson distribution for all three nights examined. On all three nights, there were more fruit with no droplets, and more fruit with large numbers of droplets than expected if the moths oviposited randomly (June 18: Dmax = 0.655, Dmax crit = 0.031, n = 1920 on 259 plants, k = 0.20; June 19: Dmax = 0.559, Dmax crit = 0.031, n = 1863 fruit on 257 plants, k = 0.13; June 20: Dmax = 0.535, Dmax crit = 0.032, n = 1773 fruit on 254 plants, k = 0.08).

The pattern of droplets on fruit just from plants with droplets also differed from a Poisson distribution for all three nights examined. Again, there were more fruit with no droplets, and more fruit with large numbers of droplets than expected if the moths oviposited randomly (June 18 Dmax = .283, Dmax crit = 0.0576, $p<0.05$, n = 556 fruit on 75 plants; k = 1.19; June 19 Dmax = 0.371, Dmax crit = 0.0578, $p < 0.05$, n = 515 fruit on 71 plants, k = 0.83; June 20 Dmax = 0.405, D-max crit = 0.07, $p < 0.05$, n = 363 fruit on 52 plants, k = 0.88) (Figure 3.1).

The pattern of droplets on fruit over time was not clumped, however. In both 1995 and 1996, fruit were more likely to be seen with droplets only once, than would be expected if the non-pollinators oviposited on fruit randomly over time (1995: Dmax = 0.074, Dmax crit = 0.039, $p < 0.05$, n = 122 fruit; 1996: Dmax = 0.058, Dmax crit = 0.038, $p < 0.05$, n = 1300 fruit). However, in both years the patterns were only just significantly different from Poisson distributions (Figure 3.2).

The pattern of non-pollinator ovipositions within fruit was not different from a Poisson distribution in 1995 (Dmax = 0.041, Dmax crit 0.122, n = 122 fruit, k = 3.29), but was clumped in 1996 (D max = 0.078, Dmax crit = 0.069, $p < 0.05$, n = 383 fruit, k = 1.13) (Figure 3.3). However, the pattern of ovipositions in locules in both years was different from random, and was clumped (1995: Dmax = 0.190, Dmax crit = 0.050, n = 733 on 122 fruit, k = 2.54; 1996: Dmax = 0.274, Dmax crit = 0.028, $p < 0.05$, n = 2299 locules on 383 fruit, k = 0.561) (Figure 3.4).

Finally, the pattern of non-pollinator larvae within fruit in both years was different from a random distribution, and was clumped (1995: Dmax = 0.227, Dmax crit = 0.039, k = 1.33, n = 122 fruit; 1996 Dmax = 0.46, Dmax crit = 0.069. k = 0.4427) (Figure 3.5). The same aggregated pattern of non-pollinator larvae was seen in locules within fruit, too (1995: Dmax = 0.049 D max crit = 0.050, n = 733 locules, k = 1.77;

1996: Dmax = 0.146, D max crit = 0.028, k = 0.518, n = 2299 locules in 383 fruit, Figure 3.5).

Non-Pollinator Choice Experiment

In the choice experiment, non-pollinator oviposition activity was not influenced by whether fruit had been oviposited in previously by another moth. On Night 2, there was no significant difference in the number of droplets on fruit that had or had not been oviposited in on Night 1 ($p = .266$, d.f. = 31, $F = 1.295$, Figure 3.6). However, the power of this analysis to detect a significant difference, given the huge variation, and poor replication was 0.

Intraspecific Competition

Survival of non-pollinator larvae appeared to decrease as the number of ovipositions per locule increased, but only when the larvae reached 4th instar. In 1995, I found that survival decreased with the number of ovipositions per locule, but this occurred only with 32 day old larvae ($n = 150$ locules, Wald = 7.0613, $p = 0.008$, Figure 3.7, Table 3.1 for all statistics). For larvae that were 8, 12, 18, and 25 days old, survival did not depend on the number of non-pollinator ovipositions. This was confirmed in 1996, as the survival of 4th instar (28 day old) non-pollinators decreased as the number of ovipositions increased ($n = 289$, $p = 0.029$, Wald = 4.75) but increased with fruit age ($p = 0.039$, $W = 4.5$) (Figure 3.8). The survival of 12 day non-pollinators did not depend on the number of non-pollinator ovipositions ($p = 0.1$, Wald = 2.72, $R = 0.04$), but did increase with fruit age ($n = 129$, $p < 0.0000$, Wald = 36.19, Figure 3.9).

In fruit collected from observations sites, a different pattern emerged in 1995 and 1996. In 1995, non-pollinator survival increased slightly as the number of ovipositions scars per locule increased ($p = 0.053$, $W = 3.73$, $R = 0.032$, $n = 335$ locules). In 1996, non-pollinator survival decreased as the number of non-pollinator oviposition scars per locule increased ($p = 0.006$, $W = 7.38$, $p = 0.007$, $R = -0.058$, $n = 408$ locules) (Figure 3.10). Once locules had 22 oviposition scars in them, survival decreased by 33%. However, at Yellow Jacket in 1995, only 4.2% of locules used by non-pollinators had 22 or more ovipositions (21/491), and in 1996 only 3.3% (55/1657) of the locules had 22 or more ovipositions.

Intraspecific larval density had little or no affect on the weight of non-pollinators ($r^2 = 0.05$, d.f. 59, $F = 1.54$, $p = 0.04$; Figure 3.11), and also had no affect on the number of seeds destroyed ($p < 0.0000$, $r^2 = 0.30$, d.f. = 96, $F = 40.66$; Figure 3.12).

Discussion

In this chapter, I described the distribution of non-pollinator oviposition patterns, and examined the role of intraspecific competition in limiting the exploitation of the yucca-yucca moth mutualism by non-pollinators. Patterns of non-pollinator ovipositions and larvae were highly aggregated in space, enhancing the opportunity for intraspecific competition. However, intraspecific competition appears to play only a small role in regulating non-pollinator numbers, and therefore limiting exploitation of the mutualists.

Non-pollinator Oviposition Patterns

The distribution of droplets on the observation sites suggests that non-pollinator oviposition patterns are aggregated. On any given morning, droplets were seen on some plants, and not on others, which alone would produce a clumped distribution of droplets on fruit. However, even within plants with droplets, the distribution of droplets was strongly aggregated. I also found that ovipositions and non-pollinator larvae were

6

aggregated within locules and fruit, suggesting that ovipositions are clumped in space over the entire season, not just on a nightly basis.

The aggregation of non-pollinator ovipositions in space, coupled with observations of non-pollinator oviposition activity (personal observations), suggests that moths make no attempt to distribute their eggs evenly in fruit. The reason for this aggregation may be that survival of non-pollinator eggs is so low, that the risk of a moth's progeny competing with one another in fruit is minimal. If the risk of competition between siblings is low, then it may be more profitable to exploit fruit heavily, and minimize any costs associated with searching for other fruit, such as additional energy expenditure, and increased risk of predation (Wilson 1988).

Interestingly, the pattern of non-pollinators in fruit was even more aggregated than the ovipositions. This pattern would not occur if non-pollinator death was simply random throughout locules, because the negative binomial description of clumping would not change (Pielou 1969). An increase in aggregation is also not explained by intraspecific competition, because if intraspecific competition was driving the deaths, aggregation would appear to decrease relative to ovipositions. Rather, two possible explanations are: 1) that non-pollinators do not lay eggs every time they insert their ovipositors, and lay proportionately more eggs in "good sites", and 2) that interspecific competition with pollinator larvae is driving the pattern (see Chapter 2). If there are three or more pollinator larvae in a locule, survival of non-pollinators is less than 5%. Thus, in locules where there are many pollinators, virtually all non-pollinator larvae are wiped out, while in locules without pollinators, survival approaches 20%. Since pollinator larvae are also aggregated in space (personal observations), this would tend to create a highly aggregated distribution of surviving non-pollinator larvae.

While the distribution of non-pollinator ovipositions is aggregated in space, there is weak evidence that moths tend toward a more uniform distribution of ovipositions over time. Over the course of one night, records of droplets suggest that moths oviposit extensively in fruit on particular plants, and completely ignore fruit on other plants. Over the course of the entire season, though, there was a greater than expected frequency of fruit that had droplets only once. It is possible that moths cue into droplets left on fruit, and avoid fruit that have obviously been used before. If this occurs, then non-pollinators may be ovipositing in a way that conforms to theories on optimal clutch sizes in insects when many females oviposit per patch (Ives 1989, Parker and Begon 1986, Holmes 1972, but also see Ives 1989 and Skinner and Mandracchia 1985). Theory suggests that under certain conditions, it is better for a female to lay few or no eggs if she is not the first to oviposit in a patch. The conditions under which this should occur are that: 1) resources within a patch are limiting, 2) females can assess egg loads, or at least determine if the patch has been used before, 3) there is an advantage to being first in a patch, and 4) little time or energy is required to find another patch. All four of these conditions hold in the yucca-yucca moth system, as competition does occur within fruit, densities of yuccas are high, so it should not take non-pollinators long to find "fresh" fruit, older larvae have a competitive advantage over smaller larvae, and (perhaps) non-pollinators can cue in on droplets to assess egg loads in fruit.

The results of the choice experiment do not support these ideas, however. In the choice experiment, there was no difference in the number of droplets that previously "hit" and "unhit" fruit received on the second night of the experiment. However, I can conclude little from that experiment because a) it was poorly replicated, b) moths may not behave normally when they are caged on yuccas, and c) this experimental situation probably does not represent a realistic situation. Normally, non-pollinators oviposit extensively on most if not all fruit on a plant and then fly to a distant plant (personal observations, Addicott unpublished results). This suggests that moths may make their decision to oviposit at the level of the plant, rather than at the level of the fruit. In the experiment, the moths were confined to one plant, and perhaps oviposited in all fruit because they actually had no choice.

I did not set out to determine the "optimal clutch size" of non-pollinators, and as a result, my data and analysis on this subject are very preliminary. However, there is a great opportunity here to explore optimal clutch sizes in insects not only when multiple females of a single species lay in a patch, but also when multiple females of several species oviposit in a patch. Indeed, since interspecific competition (Chapter 2) lowers non-pollinator survival much more strongly than intraspecific competition, the presence and/or density of pollinator larvae in fruit may influence patterns of non-pollinator larvae. Indeed, the aggregated pattern of non-pollinator and pollinator larvae, may be very important in leading to the coexistence between pollinators and non-pollinators (Atkinson and Shorrocks 1981, 1984). These and many other questions about non-pollinator oviposition strategies should be addressed in future studies.

Intraspecific Competition

I expected to see strong intraspecific competition between non-pollinators because of the aggregated pattern of ovipositions in fruit, previous reports of high numbers of non-pollinators per fruit (Addicott 1996), and the fact that yucca fruit are small, ephemeral, spatially restricted resources (Averill and Prokopy 1987, Thompson 1983, Roitberg and Prokopy 1987). In fruit from both observation sites, competition was neither as intense, nor as prevalent as I expected. While the effect of crowding was strong, with a 33% decrease in survival when there were 22 ovipositions per locule, less than 5% of the locules used by non-pollinators have this many oviposition scars.

One reason that non-pollinator survival did not appear to decrease strongly with the number of oviposition scars, is that there may be problems with estimating survival by comparing the proportion of oviposition scars associated with larvae in a locule. If moths do not lay an egg every time they insert their ovipositor, or do not at least lay an egg at a constant proportion of ovipositor insertions, oviposition scars cannot be used as a means of measuring the potential for competition. It is possible that non-pollinators do not lay eggs every time they insert their ovipositor into the fruit, and instead use their ovipositor to test potential oviposition sites, and only lay eggs in suitable sites (Odell and Godwin 1984). As well, they may be interrupted during oviposition by potential predators, or by ants seeking droplets that form on fruit, and are forced to withdraw before they have laid an egg. When I did attempt to determine the probability that an oviposition scar is associated with an egg in locules with 5 or fewer oviposition scars, I found that only 25% of these scars were associated with an egg 6 days after the moths had oviposited.

While ovigesturing is a potential source of error, I feel that oviposition scars can be used as an indication of the level of competition in a locule or fruit, provided that I keep fruit age constant (see below). In both 1995 and 1996, I found no significant decrease in the apparent survival of younger instars (Figures 3.1 and 3.3) as the number of ovipositions per locule increased, but did find a decrease in the survival of fourth instar. If non-pollinators were laying eggs at a lower proportion in fruit with many previous oviposition scars, survival would have appeared to decrease at all larval stages.

The dissections of fruit from observation sites demonstrate that intraspecific competition can occur between non-pollinators, while results from the experiments provide clues as to when it occurs. Intraspecific competition only had a noticeable affect on the survival of fourth instar larvae. This is likely due to the pattern of seed consumption by larvae of different ages. Seed consumption by non-pollinators seems to increase almost exponentially; third instar larvae usually eat a small fraction of 6 or fewer seeds in their lifetime (Chapter 2), but by the time they reach middle to late fourth instar, they eat virtually all of about 15 seeds. It is therefore unlikely that younger instar larvae can limit the food available to their neighbours, while a fourth instar larvae certainly can. The age at which intraspecific competition occurs may also explain why I did not see an affect of intraspecific competition on non-pollinator survival in 1995. In 1995, I did not attempt to harvest only fruit with mature fourth instar non-pollinators as I did in 1996. Instead, I collected fruit with non-pollinators ranging from first to fourth instar, only a few of which were 28 days old. However, I cannot explain why survival seemed to increase with the number of non-pollinator oviposition scars in 1995 (Figure 3.10).

Differential seed consumption by larvae of different ages should lead to asymmetrical competition, in which younger individuals should have little or no affect on the survival of older ones as has been seen in previous studies (Averill and Prokopy 1987, Salt 1961, Rubenstein 1981, Persson 1983, Beaver 1974, Fisher 1961, Sih 1982). This would confer an advantage to the larvae of females who laid eggs early in fruit, while the larvae of non-pollinators who lay eggs very late in the season could then be at greater risk of competition from older non-pollinators. At high non-pollinator densities, intraspecific competition could be a strong force selecting against very late non-pollinator emergence. As a result, there could be several selective forces acting to shorten the window of non-pollinator emergence: Non-pollinators would be selected against emerging too early in the yucca flowering season, because they would be forced to oviposit in young fruit that are at high risk of abortion (Chapter 2), and they would be selected against emerging late because of competition. However, the density of non-pollinator larvae in fruit was quite low, and I expect that in general intraspecific competition plays a small role in regulating non-pollinator emergence.

Density-dependent intraspecific competition can affect organisms in ways other than by just lowering their survival. Takahashi (1961) suggested that competition may also decrease body size, fecundity and adult longevity, and increase the developmental period and (for some insects) the number of instars before reaching maturity. In this study, however, I found no effect of intraspecific competition on larval seed destruction/consumption, or larval weight. This could be because I did not quantify the proportion of individual seeds that were destroyed, and since larvae eat a larger proportion of seeds as locules get more crowded, this could explain why larvae in more crowded locules did not damage significantly fewer seeds (Chapter 2). As well, much of the variation in larval weight is likely due to differences in weights of male and female non-pollinators, with females of the same age probably being as much as 30% heavier than males (personal observations). However, I could not sex the larvae by either their head capsule size or their weight, so I grouped them together in this analysis. Had I been able to distinguish between male and females, much of the variation in weight would have been accounted for, and the effect of both interspecific competition (Chapter 2) and intraspecific competition on larval weight may have been stronger.

Finally, one surprising finding of both the intra- and interspecific competition (see Chapter 2) studies was that non-pollinator survival appeared to increase significantly with fruit age. My explanation of this pattern when pollinator larvae were present was that survival increased with the age difference between yucca moth larvae and non-pollinators, because yucca moth larvae would emerge sooner with respect to the non-pollinator larvae, and the two species of larvae would have less time to interact and compete. However, this does not explain why survival is significantly higher in older fruit without yucca moth larvae. My only explanation is that these results are an artifact of non-pollinator oviposition behaviour. As I suggested above, non-pollinators females probably do not lay eggs every time they insert their ovipositor, and in older fruit they may be more likely to actually lay an egg when they insert their ovipositor, because these fruit are more likely to be retained. Perhaps the moths can sense the age of a fruit by the toughness of the seeds, and because young fruit are more likely to be aborted than older fruit, they are less likely to lay an egg in young fruit. At this point, however, this is simply speculation, and further studies are needed to determine the process that leads to higher apparent survival in older fruit.

Literature Cited

Addicott, J. F. 1986. Variation in the costs and benefits of mutualism: The interaction between yuccas and yucca moths. *Oecologia* 70: 486-494.

———. 1996. Cheaters in yucca/moth mutualism. *Nature (London)* 380: 114-15.

Addicott, J. F. and A. J. Tyre. 1995. Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72: 382-94.

Addicott, John F. Bronstein Judith and Finn Kjellberg. 1990. Evolution of Mutualistic Life-Cycles: Yucca Moths and Fig Wasps. *Insect Life Cycles.* 1 ed., Editor Francis Gilbert, 143-61. London: Springer-Verlag.

Atkinson, W. D. and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: A simulation model. *Journal of Animal Ecology* 50: 461-71.

———. 1984. Aggregation of larval diptera over discrete and ephemeral breeeding sites: The implications for coexistence. *The American Naturalist* 124, no. 3: 336-51.

Averill, A. L. and R. J. Prokopy. 1987. Intraspecific competition in the tephritid fruit fly *Rhagoletis pomonella*. *Ecology* 68, no. 4: 878-86.

Axelrod, R. and D. Dion. 1988. The further evolution of cooperation. *Science* 242: 1385-90.

Beaver, R. A. 1973. The effects of larval competition on puparial size in Sarcophaga spp. (Diptera:Sarcophagidae) breeding in dead snails. *Journal of Entomology (A) General Entomology* 48: 1-9.

Bultman, T. L. and P. L. Mathews. 1996. Mycophagy by a millipede and its possible impact on an insect-fungus mutualism. *Oikos* 75, no. 67: 74.

Bultman, T. L. 1995. Mutualistic and parasitic interactions between *Phorbia* flies and *Epichloe:* convergence between a fungus and entomophilous angiosperms. *Canadian Journal of Botany* 73, no. supplemental 1: S1343-S1348.

Credland, P. F. Dick K. M., and A. W. Wright. 1986. Relationship between larval density, adult size and egg production in the cowpea seed beetle *Callosobruchus maculatus*. *Ecological Entomology* 10: 225-30.

Feder, J. L., Reynolds K., Go W., and E. C. Wang. 1995. Intra- and interspecific competition and host race formation in the apple maggot fly, *Rhagoletis pomonella* (Diptera:Tephritidae). *Oecologia* 101: 416-25.

Ferriere, R. and R. E. Michod. 1996. The evolution of cooperation in spatially heterogeneous populations. *The American Naturalist* 147, no. 5: 692-717.

Fisher, R. C. 1961. A study in insect multiparasitism.II. The mechanism and control of competition for possesion of the host. *Journal of Experimental Biology* 40: 531-40.

Holmes, H. B. 1972. Genetic evidence for fewer progeny and a higher percent males when Nasonia vitripennis oviposits in previously parasitized hosts. *Entomophaga* 17: 79-88.

Houston, A. I. 1993. Mobility limits cooperation. *Trends in Ecology and Evolution* 8: 194-96.

Ives, A. R. 1989. The optimal clutch size of insects when many females oviposit per patch. *The American Naturalist* 155, no. 5: 671-87.

Keeley, J. E., Keeley S. C., and D. A. Ikeda. 1986. Seed predation by yucca moths on semeparous, iteroparous and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). *The American Midland Naturalist* 115, no. 1: 1-9.

Kerdelhue, C. and J. Rasplus. 1996. Non-pollinating Afrotropical fig wasps affect fig-pollinator mutualism in Ficus within the subgenus Sycomorus. *Oikos* 75: 3-14.

Messina, F. J. and J. A. A. Renwick. 1985. Ability of ovipositing seed beetles to discriminate between seeds with differing egg loads. *Ecological Entomology* 10: 225-30.

Morris, W. F. 1996. Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology* 77, no. 5: 1451-62.

Odell, T. M. and P. A. Godwin. 1984. Host selection by *Blepharia pratensis* (Meigen), a tachinid parasite of the gypsy moth, *Lymantria* L. *Journal of Chemical Ecology* 10, no. 2: 311-20.

Parker, G. A. and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *The American Naturalist* 128: 573-95.

Pellmyr, O., Leebens-Mack J., and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-56.

Persson, L. 1983. Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos* 40: 197-207.

Pielou, E. C. 1969. *An Introduction to Mathematical Ecology*. New York, USA: John Wiley and Sons.

Powell, J. A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7, no. 1: 10-14.

Prokopy, R. J. 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. *Environmental Entomology* 1: 326-32.

Prokopy, R. J. Ziegler J. R. and T. T. Y. Wong. 1978. Deterrence of repeated oviposition by fruit-marking pheromone in Ceratitis capitata. *Journal of Chemical Ecology* 4: 55-63.

Riley, C. V. 1892. The yucca moth and yucca pollination. *Annual Report of the Missouri Botanical Garden* 3: 99-159.

Roitberg, B. D. and R. J. Prokopy. 1987. Insects that Mark Host Plants. *BioScience* 37, no. 6: 400-406.

Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63, no. 2: 354-60.

Roubik, D. W., Holbrook N. M., and German P. V. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161-67.

Rubenstein, D. I. 1981. Individual variation and competition in the Everglades pygmy sunfish. *Journal of Animal Ecology* 50: 337-50.

Salt, G. 1961. Competition among insect parasitoids. *Symposia of the Society for Experimental Biology* 15: 98-119.

Shapiro, A. M. 1981. The pierid red-egg syndome. *The American Naturalist* 117, no. 3: 276-94.

Shorrocks, B. 1990. Competition and selection in a patchy and ephemeral habitat: The implications for insect life-cycles. *Insect Life Cycles: Genetics, evolution and co-ordination.* editor Francis Gilbert, 215-28. London, UK: Springer-Verlag.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmani*. *Ecology* 63, no. 3: 786-96.

Skinner, M. C. and J. Mandracchia. 1985. Clutch size as an optimal foraging problem for insect parasitoids. *Ecological Entomology* 17: 231-38.

Smith, R. H. and C. M. Lessells. Oviposition, ovicide and larval competition in granivorous insects. *Behavioural ecology: ecological consequences of adaptive behaviour.* editors R.M. Sibly and R.H. Smith, 423-48.

Soberon Mainero, J. and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic systems. *The Biology of Mutualism.* editor D. H. Boucher, 192-216. London: Croom Helm.

Stiling, P. D. and D. R. Strong. 1983. Weak competition among Spartina stem borers, by means of murder. *Ecology* 64: 770-778.

Thompson, J. N. 1983. Selection pressures on phytophagous insects feeding on small host plants. *Selection pressures on phytophagous insects feeding on small host plants.* 40: 438-44.

Tyre, A. J. and J. F. Addicott. 1993. Facultative non-mutualistic behaviour by an "Obligate" mutualist: "Cheating" by yucca moths. *Oecologia* 94: 173-75.

West, S. A. and E. A. Herre. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London B.* 258: 67-72.

Wilson, K. 1988. Egg laying decisions by the bean weevil *Callosobruchus maculatus*. *Ecological Entomology* 13: 107-18.

Zar, J. H. 1984. *Biostatistical Analysis*. New Jersey, USA: Prentice Hall.

Table 3.1: Results of 1995 intraspecific competition logistic regression analyses.

Variable	b	Wald	p	R	n
Eggs	-0.380	0.866	0.352	0.000	131
Constant	-0.910	14.185	0.0002		
First Instar	-0.006	0.157	0.692	0.000	138
Constant	-0.850	22.570	0.0000		
Second Instar	-0.041	1.758	0.185	0.000	134
Constant	-0.860	13.631	0.0002		
Third Instar	-0.044	0.677	0.411	0.000	135
Constant	-0.827	8.697	0.003		
Fourth Instar	-0.063	7.061	0.008	-0.097	199
Constant	-1.951	60.952	0.0000		

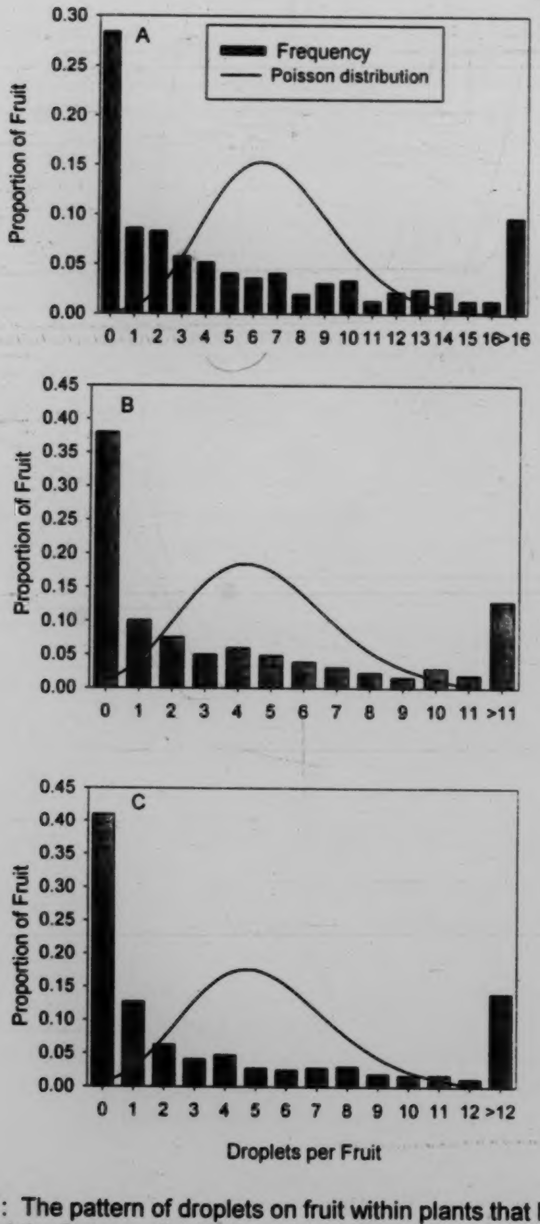

Figure 3.1: The pattern of droplets on fruit within plants that had at least one droplet and the Poisson distribution of droplets on fruit on A) 18 June, B) 19 June, and C) 20 June 1996.

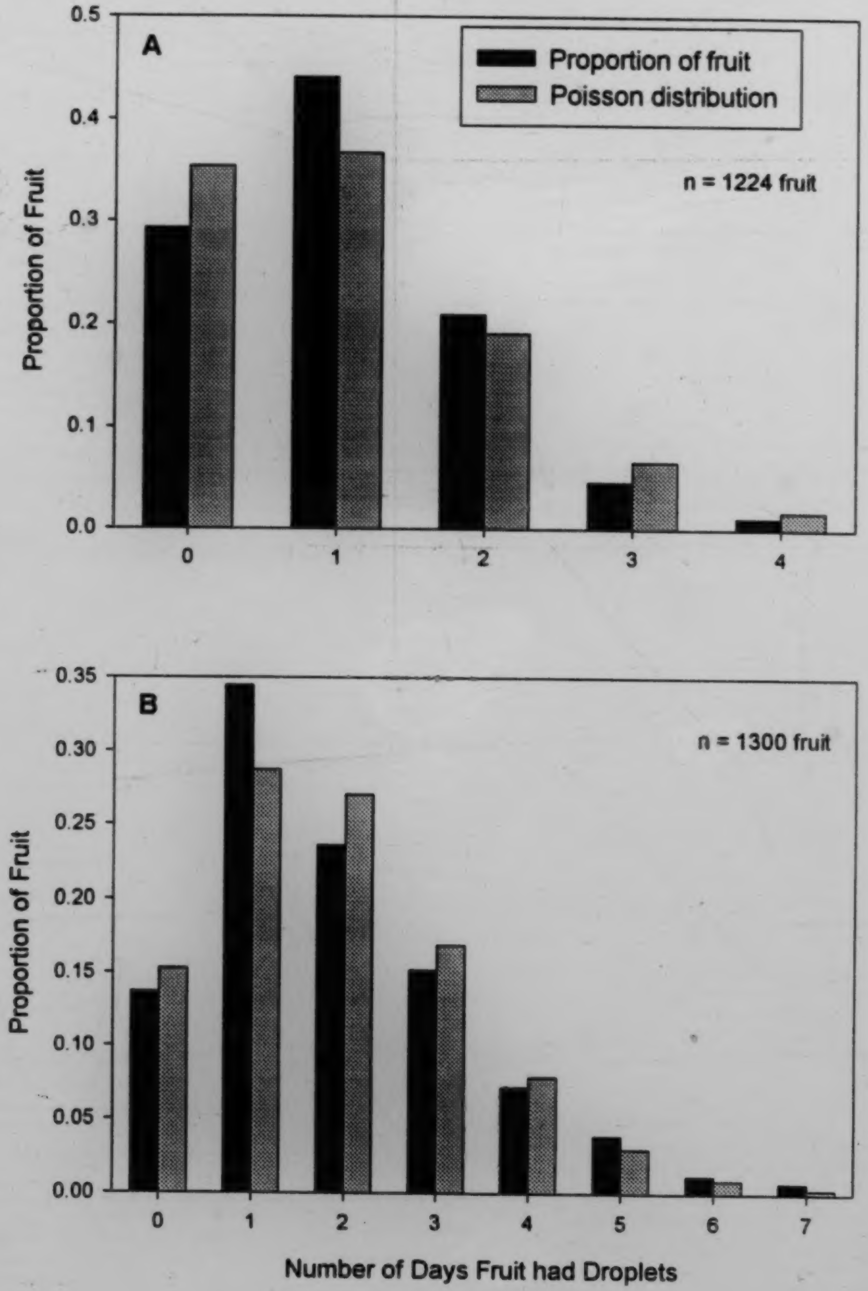

Figure 3.2: Proportion of fruit that were seen with droplets a given number of times in A) 1995 and B) 1996.

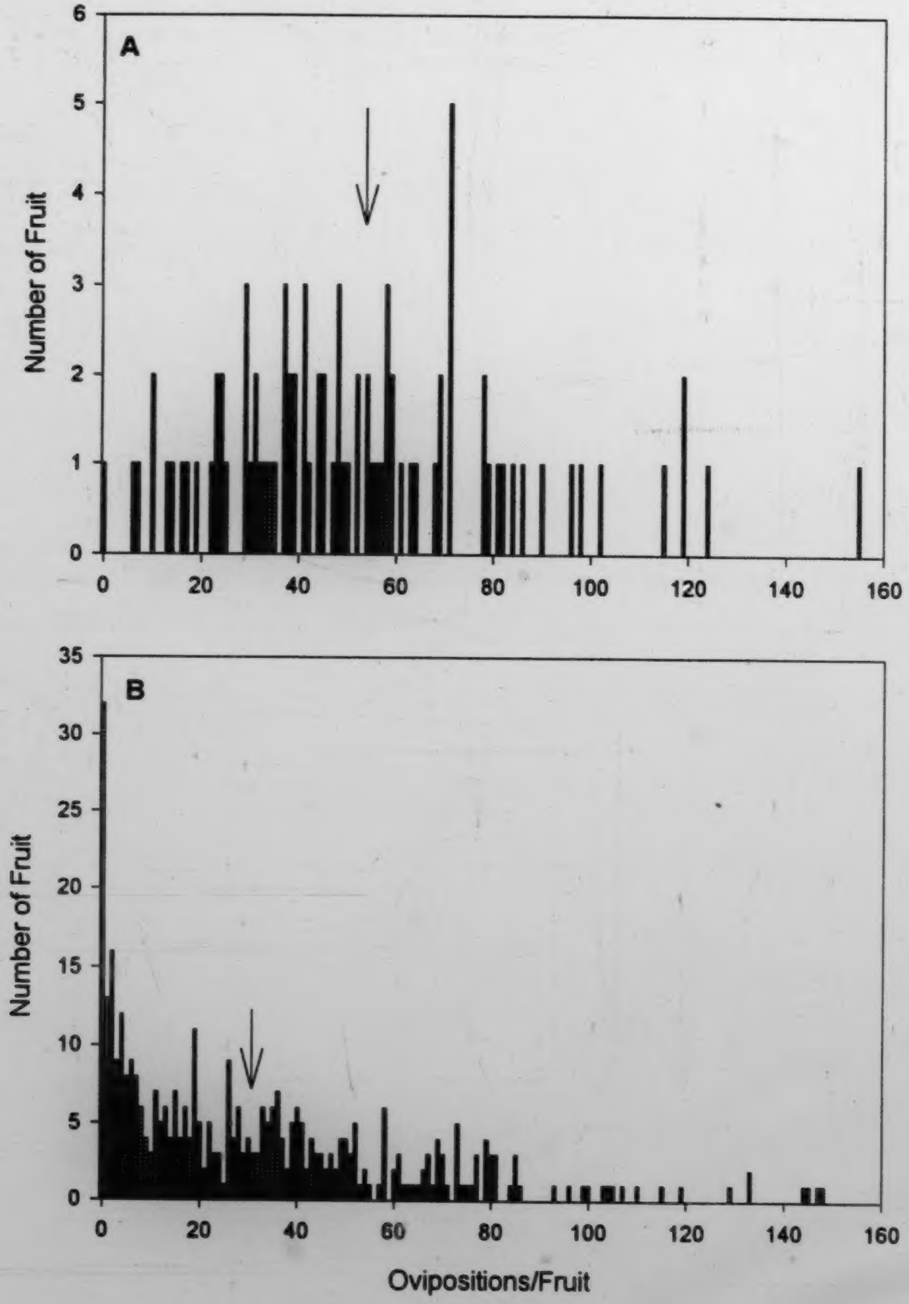

Figure 3.3: Number of fruit with a given number of non-pollinator oviposition scars collected from observation sites in A) 1995 and B) 1996. Arrows indicate the mean number of ovipositions per fruit at each site.

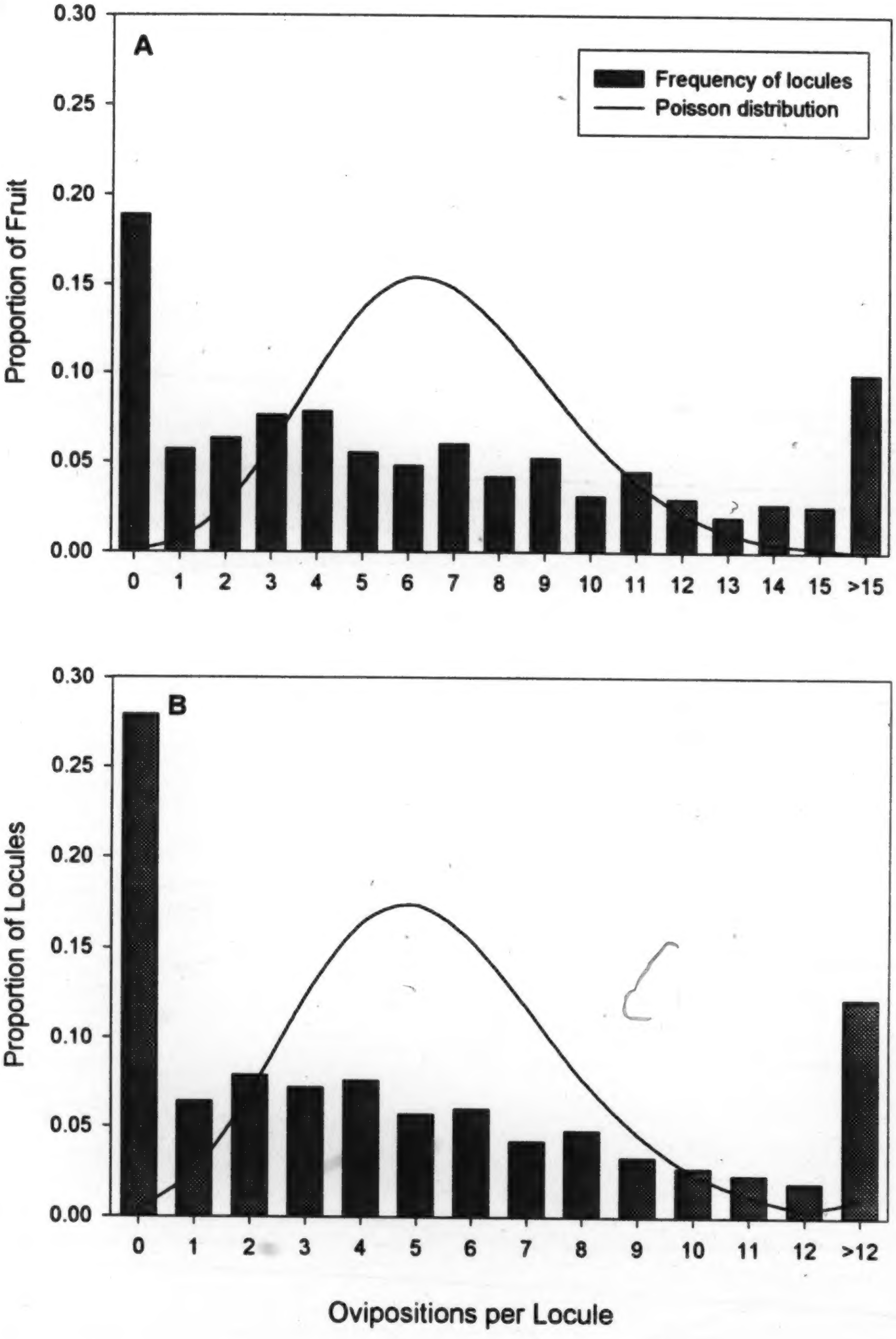

Figure 3.4: The proportion of locules with given numbers of non-pollinator oviposition scars as compared to a Poisson distribution in A) 1995 and B) 1996.

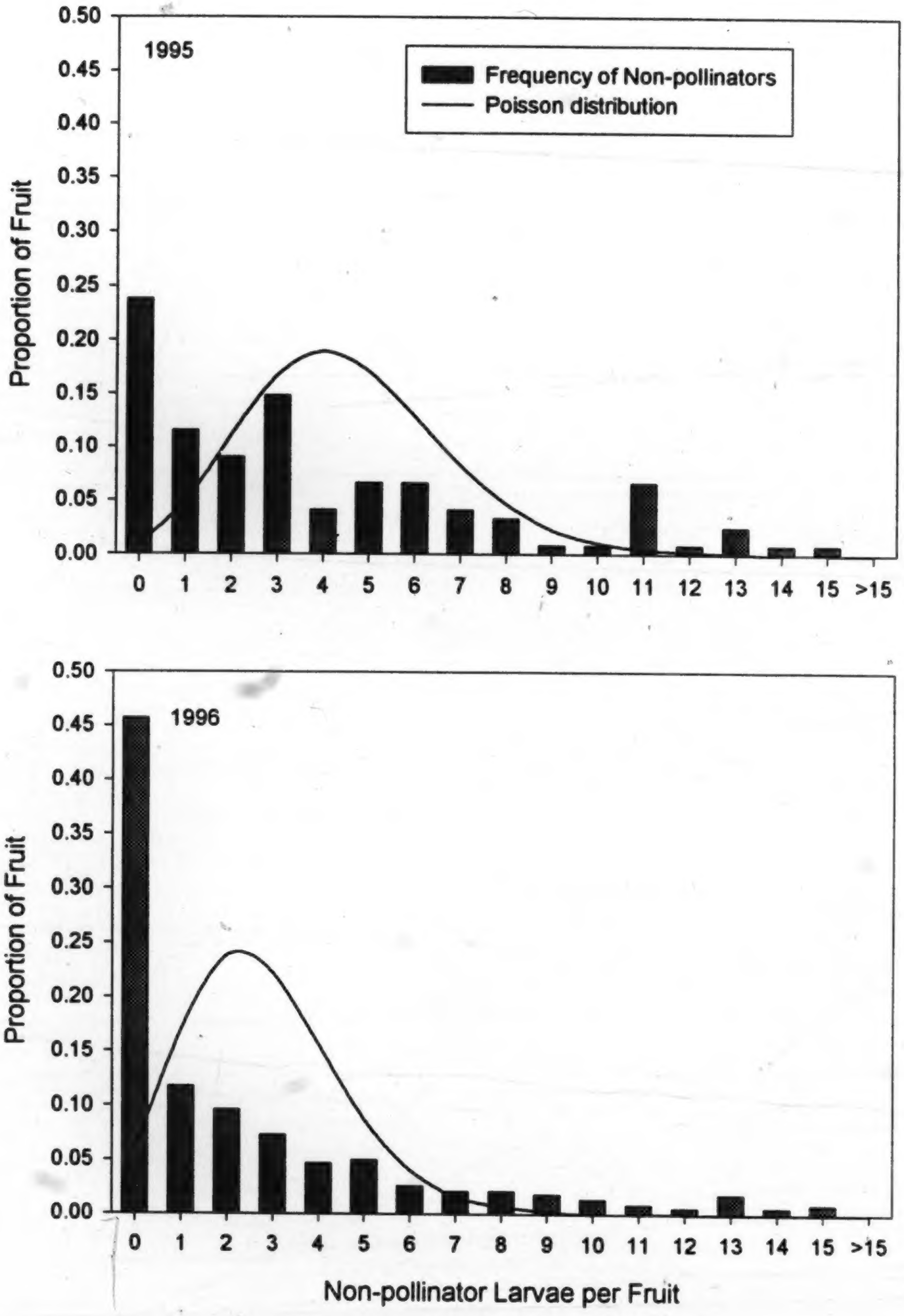

Figure 3.5: Proportion of fruit with given numbers of non-pollinator larvae in fruit collected from observation sites in A) 1995 and B) 1996. Black bars indicate the frequency of collected fruit, grey bars show a random distribution.

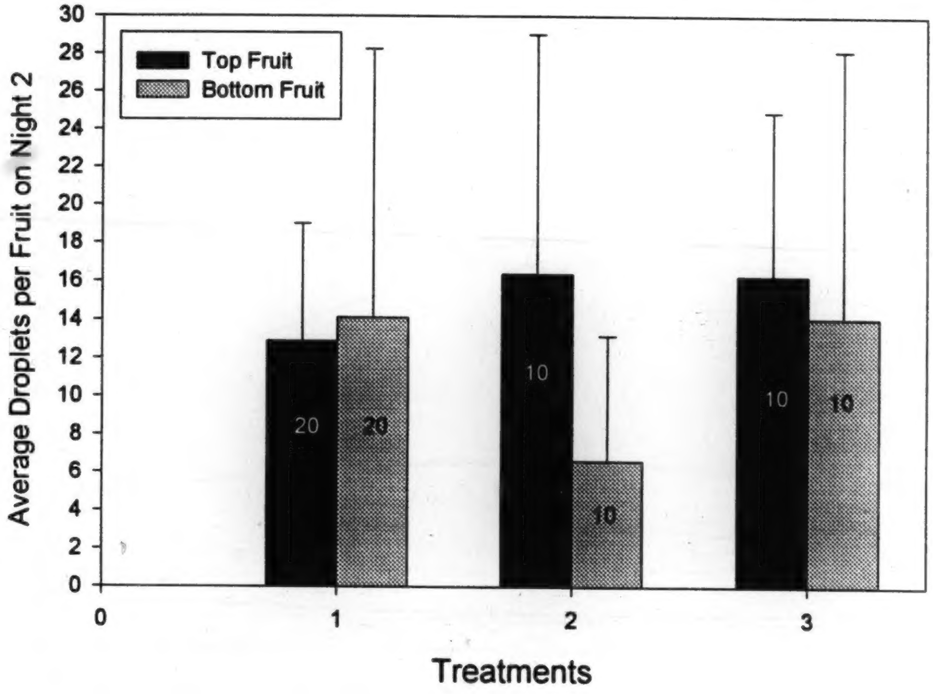

Figure 3.6: The average number of droplets on top and bottom fruit on night 2 of the Choice experiment. (1 = control, 8 replicates; Treatment 2 = top fruit hit on night 1, 4 replicates; Treatment 3 = bottom fruit hit on night 1, 4 replicates; number of fruit per treatment given in bars).

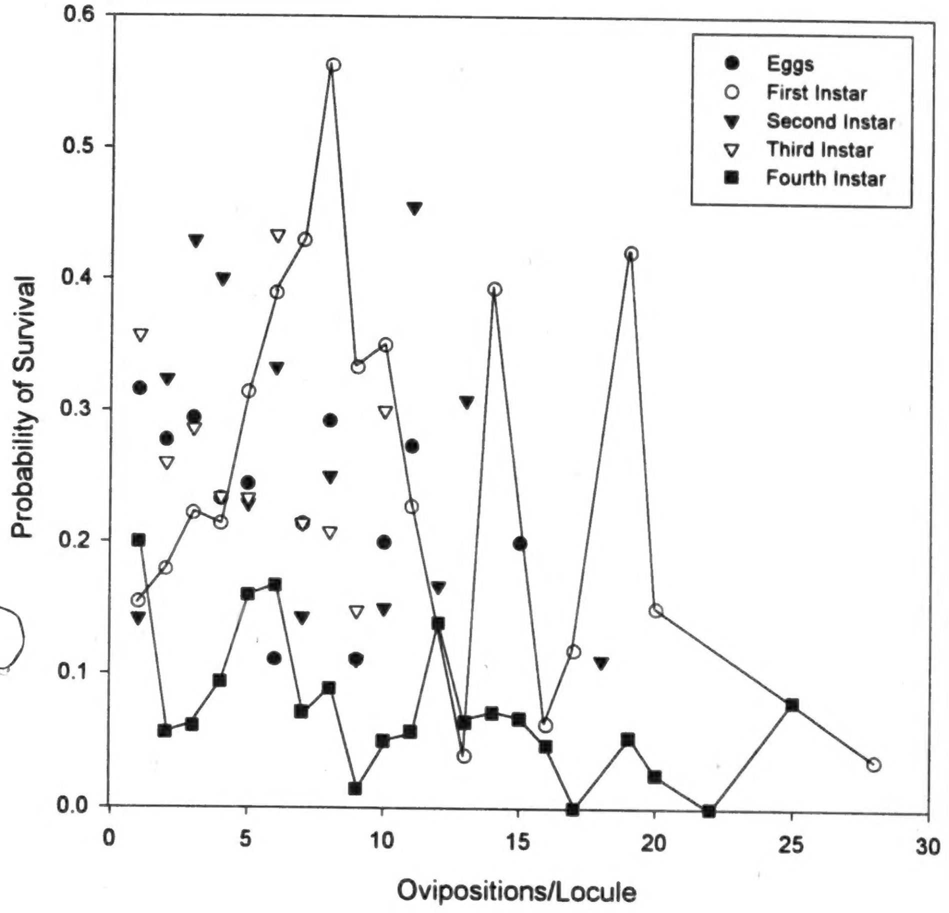

Figure 3.7: The proportion of ovipositions associated with non-pollinator larvae (survival), in locules with increasing numbers of ovipositions. Lines illustrate the difference in survival of first and fourth instar larvae.

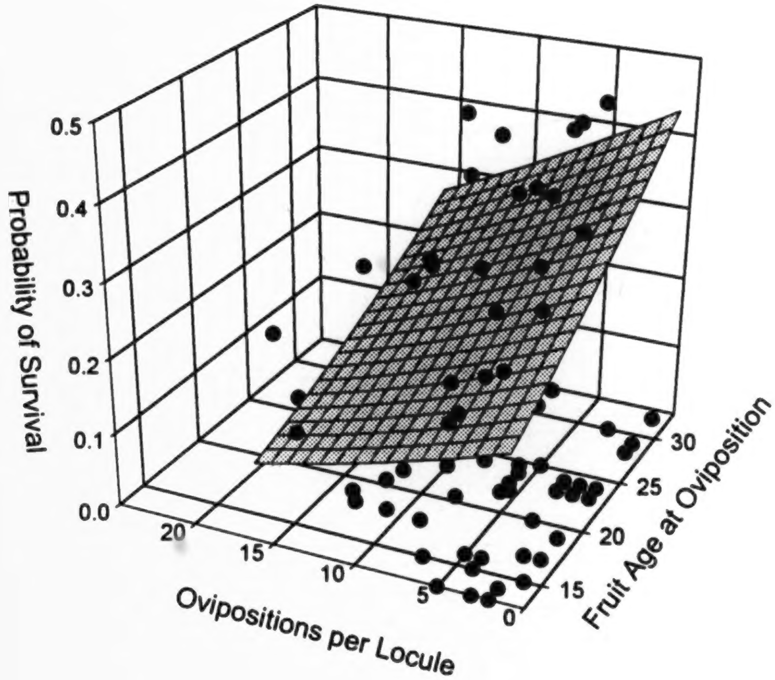

Figure 3.8: The probability that non-pollinator oviposition scars are associated with 28 day old non-pollinator larvae (survival) as a function of the age of fruit at oviposition, and the number of ovipositions per locule. Surface plot represents the probability of survival predicted by logistic regression model; symbols represent the average probability of survival in locules with a given number of ovipositions scars at a given fruit age. $y = 1/1+e^{(-(2.108 - (0.048 * \text{Ovipositions})+(0.057 * \text{Fruit Age})}$

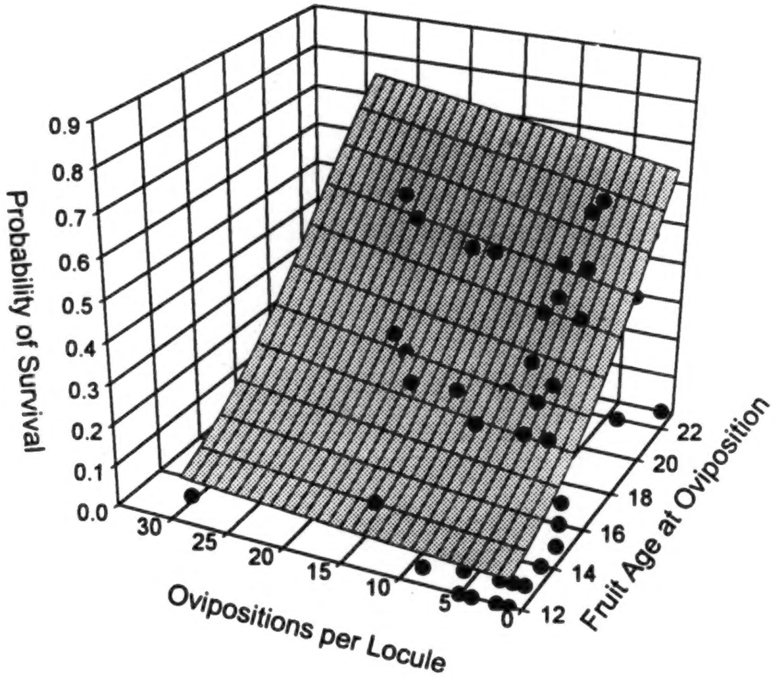

Figure 3.9: The proportion of non-pollinator oviposition scars associated with 12 day old non-pollinator larvae (probability of survival) as a function of the number of ovipositions per locule and the age of fruit at non-pollinator oviposition. Surface plot represents the probability of survival predicted by logistic regression; symbols represent the average survival in locules with given numbers of oviposition scars at a given fruit age.
$y = 1/1+\exp^{(-(-6.17+(0.02^{*}\text{Ovipositions})+(0.29^{*}\text{Fruit Age})}$.

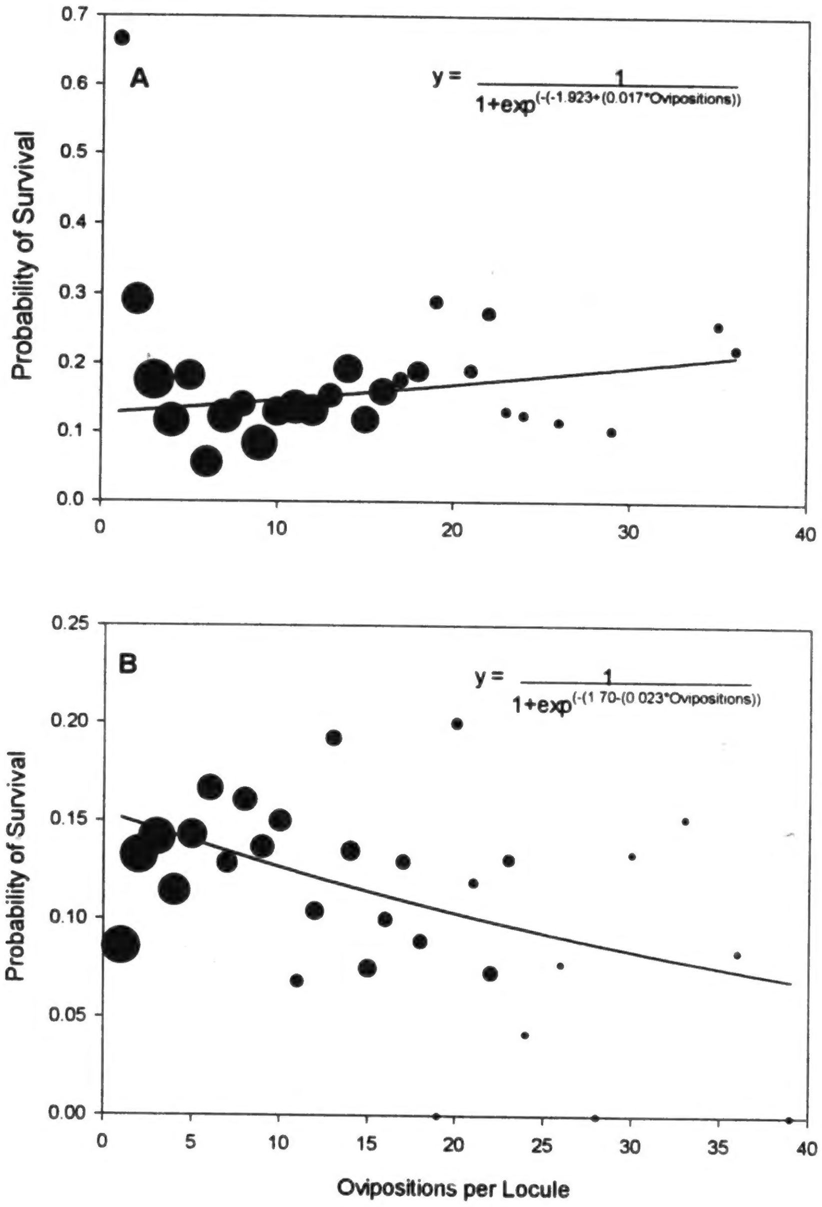

Figure 3.10: Proportion of oviposition scars in a locule associated with a non-pollinator larvae (probability of survival) as a function of the number of non-pollinator oviposition scars. Circles represent the average survivorship in locules with given numbers of oviposition scars; circle size is proportional to sample size. A) 1995 B) 1996 (see text for details).

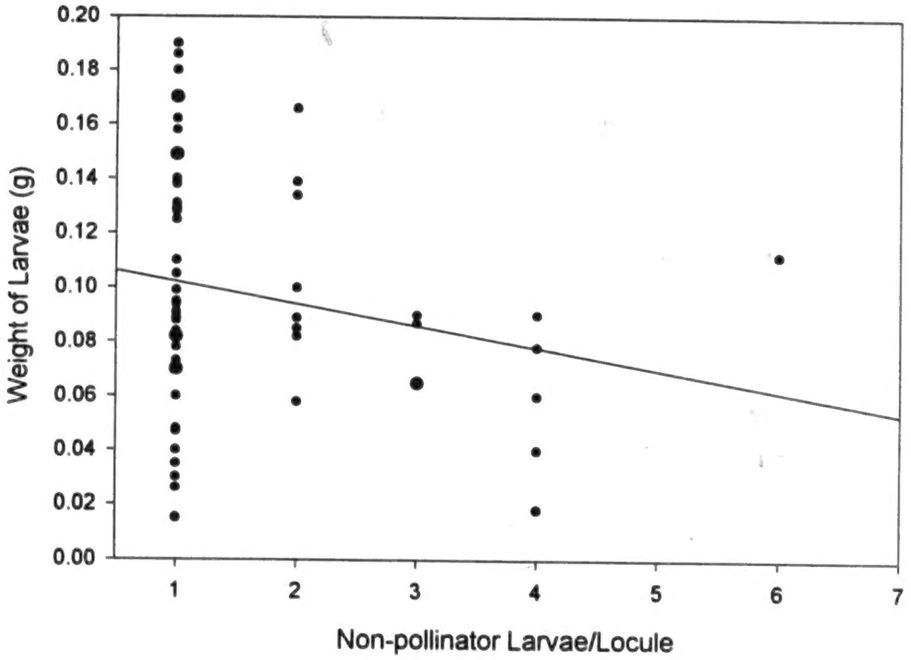

Figure 3.11: Weight of fourth instar non-pollinator larvae as a function of the number of fourth instar non-pollinator larvaea per locule.

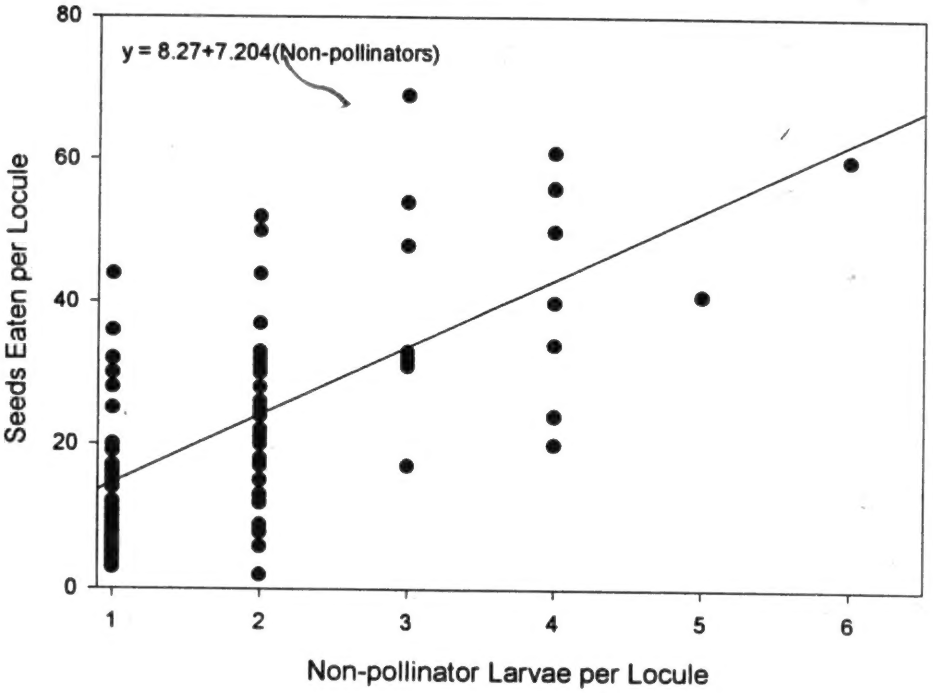

Figure 3.12: The number of seeds eaten in a locule as a function of the number of fourth instar non-pollinator larvae per locule.

Chapter 4

Life History Synchronization and Yucca Population Structure

Abstract

Many mutualists are exploited by organisms who benefit from mutualistic resources, but provide no benefit in return. In some systems, where the exploitation can be severe, and potentially disruptive to the mutualism, mutualists and their exploiters appear to have coexisted for a long time. This suggests that there are processes that limit the effect of exploiters on mutualists. In this study, I test the hypothesis that the population structure of mutualists in space and time makes some mutualists more vulnerable to exploitation, but allows others to escape. I examine the exploitation of the mutualism between the yucca plant, *Yucca kanabensis*, and it's pollinator (*Tegeticula yuccasella* spp.), by a non-pollinating yucca moth. Specifically, I examine 1) the longevity of the non-pollinating moth, 2) synchrony between non-pollinator emergence and yucca fruiting, 3) the effect of fruit age on non-pollinator oviposition activity and 4) the effect of plant isolation on non-pollinator oviposition activity.

I found that asynchrony of yucca plant fruiting and non-pollinator emergence did not limit exploitation in either year of study. In both years, non-pollinator emergence was very well timed with the initiation of mature fruit in which the moths oviposit. As well, non-pollinator females live up to an average of 12 days when flowers are available for them to rest in, and an average of 8 days when flowers are not available. As a result, even if non-pollinators emerged very early, they would probably live until fruit were available on the site.

The population structure of yuccas may play a small role in limiting exploitation of yuccas. Plants that are isolated in space may escape non-pollinator attacks, but only if the isolation is extreme (>100m from the nearest neighbour). Plants that are isolated in time may also escape in space, with extremely young or extremely old fruit not being available to non-pollinators who prefer to oviposit in fruit from 8 to 30 days old.

Introduction

Two problems in ecology arise from the simple observation that to be successful, exploiters must occur at the same time and place as their "victims". One is the study of the synchronization of the life cycles of interacting organisms (Addicott 1990; Herrera 1990; Solbreck et al. 1990; Bradshaw 1990), and the other is the study of how the distribution of one organism in space influences how it is used by another (Fretwell 1972; Parker and Sutherland 1986; Parker and Stuart 1976; Halley and Dempster 1996; Levine and Wetzler 1996). In this chapter, I consider how the synchrony of life histories and population structure influence the degree to which mutualists, and more specifically, parasites of mutualists, exploit one another.

The synchrony of life cycles of mutualists can be examined on at least two scales. First, synchrony can be examined on a seasonal or yearly scale to determine the extent to which life cycles of mutualists overlap throughout the year (Addicott et al. 1990; McKey 1989; Murphy and Schauer 1996; Subramanya and Radhamani 1993). This tells us if an interaction between potential mutualists is even possible. Second, synchrony can be examined within a season, to determine if more subtle patterns influence the likelihood that mutualists interact (Herrera 1990; Roubik 1982; McKey 1989). On either scale, two factors that may influence the degree of synchrony between mutualists are: 1) the degree to which the mutualists depend on one another, and 2) the degree to which their life cycles are seasonal (Addicott et al. 1990).

If a mutualism is obligate for one or both mutualists, there should be strong selection for synchrony of life cycles. For instance, in many orchid-pollinator interactions, orchids are obligately dependent on their pollinators. Even though the pollinators may not rely on the orchids, orchid flowering corresponds closely with peak pollinator activity (House 1993; Nilsson 1992; Ackerman 1983). On the other hand, if plants are pollinated by a variety of pollinators which in turn use a variety of plants, there should be little selection for the evolution of synchrony between a particular pair of mutualists (Schemske 1983; Howe 1984).

Second, synchrony between mutualists could be influenced by the seasonality of the organisms and the environment (Addicott et. al. 1990). If one or both mutualists was continuously available, there is no reason to expect selection to synchronize the life cycles. However, seasonal environments, the life cycles of mutualists should correspond tightly, or else one or both mutualists will suffer a decline in fitness (Copland and Whelan 1989).

In plant-pollinator mutualisms, for example, plants flowering either before their pollinators emerge, or after their pollinator's flight season(s) may suffer declines in pollination and subsequent seed set (Copland and Whelan 1989; Addicott et. al. 1990; Smith-Ramirez and Armesto 1994).

As with the study of the synchrony of life cycles, the distribution of mutualists in space can also be examined at a variety of scales. For instance, we can look at the presence or absence of mutualists on a large, geographic scale, and determine if one mutualist can exist in an area without the other. On a much smaller scale, though, we can examine how the distribution of one mutualist influences the distribution, and pattern of use by its partner.

On this smaller spatial scale, the density of one mutualist can affect its use by another (Breton and Addicott 1992; Aagren 1996; Sih and Baltus 1987). For example, Breton and Addicott (1992) found that the "per-aphid" tending by ants decreased as the density of aphids increased. In contrast, Sih and Baltus (1987) found that an increase in the density of host plants actually increased the pollination of plants by bumblebees and honeybees, because large patches of flowers attracted a disproportionately higher number of pollinators than plants more isolated in space.

On this smaller scale we can also see an interaction between life history synchronization and the spatial distribution of organisms. For example, mutualists may need to exploit partners at a given age or life-history stage, so their activities will be limited to those areas where mutualists of this age are located. Pollinators, for example, feed on the nectar of flowering plants. Generally, at any given time, only some plants of a given species will be in bloom. The distribution of mutualistic plants in space changes through time, and pollinator activities necessarily change with them. But depending on the proximity of these plants to such things as nesting sites, or other plants, the use of plants by pollinators may differ depending on when and where they flower. Isolated plants, for example, may never be discovered by pollinators who concentrate their foraging efforts in areas of high plant density. Similarly, isolated plants at peak season may not be discovered by foraging pollinators as pollinators will likely focus on large patches, near to nesting sites because it is efficient. At the beginning or the end of the flowering season, when flowering plants are at low density, and pollinators must forage further, isolated plants may be more likely to be discovered.

These two factors - synchrony of life cycles, and the distribution of mutualists in space - can influence the extent to which mutualists can exploit each other. But the same reasoning applies to the exploiters of mutualism as well. Parasites or exploiters of mutualisms are organisms that exploit mutualisms without providing reciprocal benefit (Soberon and Martinez 1985). Because they rely on mutualists, their life cycles should also be synchronized with mutualists, and how they use mutualists should depend on the mutualists' distribution in time and space (Louda 1982; Biere and Honders 1996).

In this chapter I examine the effects of the distribution of yuccas and yucca moths in space and time on the oviposition behaviour of a moth which exploits the mutualism. In this system, yucca moths (*Tegeticula yuccasella* spp.) actively gather yucca pollen with specialized mouth parts called maxillary tentacles. They then fly to a flower on another inflorescence, oviposit into the flower's ovary, and actively pollinate the flower (Riley 1892, reviewed in Addicott 1990, and Powell 1992). By pollinating, the moth improves the chances that the flower will be retained as fruit, and that her progeny, which feed solely on developing yucca seeds, will survive (Keeley 1984, Addicott 1986).

In some areas, this mutualism is exploited by a non-pollinating yucca moth. These species of *Tegeticula yuccasella* are about 50% larger than the yucca moth and have vestigial maxillary tentacles, and therefore cannot carry pollen (Addicott 1990, Addicott 1996, Pellmyr et al. 1996). Moreover, they lay eggs directly in the seeds of yucca fruit that have already been pollinated, and therefore they do not pollinate.

In Chapter 2, I showed that an average of 30% of yucca seeds are lost to non-pollinators, but the distribution of non-pollinator larvae are highly aggregated: some fruit lose up to 74% of their seeds to non-pollinators, while others lose none. This is supported by previous reports of >50 non-pollinator larvae per fruit (Addicott 1996), and of significant seed losses due to non-pollinators (Pellmyr et. al. 1996). Despite the large, and potentially destabilizing effect of non-pollinators of the yucca-yucca moth mutualism, the mutualists and non-pollinator appear to have coexisted for a long time (Pellmyr et al. 1996), suggesting that there are processes that limit the damage caused by the non-pollinating moth.

The aggregated distribution of non-pollinator larvae in fruit suggests that non-pollinators moths cannot use every fruit in an area, which could limit non-pollinator exploitation of yuccas. I suggest the variation in oviposition activity is at least partly driven by the distribution of yucca fruit in time and space. The influence of the distribution of yucca fruit in time depends on both the timing of non-pollinator emergence, and the longevity of the non-pollinator. For example, in Chapter 2 I found that non-pollinators tend to oviposit in older fruit, possibly because these fruit are less likely to be aborted. If they emerge relatively early, there may be no older fruit to lay eggs in, which could dramatically reduce the fitness of an "early emerging" moth if it is short lived. However, if it is long-lived, it may be able to "wait out" the flowering season until older fruit are available.

The distribution of yuccas in space might also affect exploitation by non-pollinators. Isolated plants may be used more extensively than plants at high density because they may attract moths from a larger area (Aker and Udovic 1981), but this may depend on the age of fruit on isolated plants. At high yucca density, plants with fruit of all ages may be present in a small area, so there will be older fruit to lay eggs in on some plants, and flowers to rest and mate in on others. This may focus oviposition activity on the plants with older fruit, allowing those with younger fruit to escape exploitation. On isolated plants, though, oviposition activity might change. Non-pollinators may originally be attracted to yuccas with flowers and young fruit because yucca flowers serve as resting and mating sites, but may stay to oviposit in young fruit because there are no other fruit immediately available. Conversely, isolated plants with older fruit, may experience less exploitation than those with younger fruit, because they do not initially attract large numbers of moths.

In this chapter, I discuss the affect of the distribution of yuccas in time and space on non-pollinator oviposition patterns. First, I examine non-pollinator longevity and the synchrony of non-pollinator emergence with yucca flowering. Then, I describe two experiments in which I study the effect of plant isolation and fruit age on non-pollinator oviposition activity.

Study Site and Study Organisms

I studied interactions between yucca moths (*Tegeticula yuccasella* spp.), yuccas (*Yucca kanabensis* (McKelvey)) and a related non-pollinating moth (*Tegeticula yuccasella* spp.) (Addicott 1996) at two sites from June 12 to July 24 1995, and May 18 to July 18 in 1996. The "Yellow Jacket" site is located near Yellow Jacket Ranch near Coral Pink Sand Dunes State Park, Utah, USA. The "Old 89" site is located on the north side of the old US 89 Highway between Mt. Carmel and Kanab, Utah, USA (Addicott and Tyre 1995).

Methods

Synchronization of life history traits

a) Non-pollinator Survival

I determined the lifespan of male and female non-pollinators on yuccas with and without flowers in 1995, to determine: a) how long they can live, and b) whether the presence of flowers influences survival rates. I collected non-pollinators (See Chapter 2) and placed 5 females and 5 males in window screen cages on each of 10 plants. Five of these plants had flowers and fruit, and 5 had fruit only. In total, then, I studied 25 males and females on each type of plant. Each day I counted the number of moths that were alive and dead in cages and removed the dead ones. I also recorded whether or not a dead moth was found at the bottom of the cage (possibly a natural death), or was found dead wedged in the screening of the cage (an unnatural death). I examined survival using Kaplan Meier survival analysis, which censors the moths that died an "unnatural" death. Finally, I compared survival between females and males on the different plant types to determine if the presence of flowers increases non-pollinator longevity.

b) "Snapshots"

To determine the "yucca environment" into which the non-pollinators emerged, I recorded the number of buds, flowers, enlarging ovaries (2-6 days old), young fruit (6-12 days old), and maturing fruit (>12 days old) on the 169 yuccas of the 1995 "Yellow Jacket" observation site. In 1995, I did this twice, when males were first seen, and when females were first seen. In 1996, I only had 20 plants, but I followed every flower on these plants, from opening to abortion, so I also knew the "environment" during the peak non-pollinator flight season in 1996 - June 19.

Distribution of Non-pollinator Ovipositions in Space

Spatial Experiment

In this experiment, I compared non-pollinator droplets and ovipositions on plants that were either isolated or not isolated, and that had flowers and young fruit, or had only maturing fruit. I isolated yuccas by selecting plants in low density yucca sites, and then either cutting down, or bagging, any inflorescences within 100m of that plant. Of the isolated plants, 9 had only mature fruit at the beginning of the experiment, and 9 had both flowers and fruit up until at least 5 days into the experiment (at which point some plants began to lose their flowers). Plants in the control group were at most 15 meters from another yucca.

On each day during the non-pollinator flight season, I recorded the number of droplets on each fruit of each plant. After I counted the droplets, I washed them off with water so that I could identify new droplets the next day. Four weeks after the observations were complete, I randomly collected 2-3 fruit from each plant in the four treatments and dissected them to examine the number of ovipositions in the fruit.

I compared the proportion of fruit with droplets per plant between treatments by arcsine square root transforming the data and running a 2-way ANOVA with interaction. Then, I compared the number of ovipositions per fruit between treatments using a 2-way Kruskal Wallis with interaction.

Spatial Observations

In 1996, I followed up the spatial experiment with observations of non-pollinator oviposition activity on the Old 89 observation site. I used a Trimble Geo Explorer hand held Global Positioning System (GPS) unit to record the location of one inflorescence in each yucca clone on the site. I recorded the position of the inflorescence for 3 minutes, attaining an estimated precision of 1 meter. If there were other inflorescences in the yucca clone, I took the compass bearing and distance in meters of those plants from the one I measured with GPS. In total, I recorded the positions of 279 inflorescences.

I downloaded the data from the GPS unit using GEO-PC software and differentially corrected the data using base station data from Flagstaff, Arizona provided by the Colorado Plateau Information Network.

I also recorded which plants started to bloom or finished blooming on a given day. This gave me a crude estimate of fruit age on plants. Plants that bloomed first generally had older fruit, as most fruit is set near the bottom or middle of the plant (Addicott and Humphries, unpublished).

Finally, for each day during the non-pollinator flight season, I visited the observation site from 6:00am to 10:00 am and counted all of the droplets on all fruit that had droplets, to determine which fruit had been visited by the non-pollinators. Making these observations early in the morning reduced the chance that the droplets would be either eaten by insects, or washed away by thunderstorms before I counted them.

To analyze these data, I used multiple regression to determine if the following variables explained variation in the proportion of nights that a plant had droplets: 1) the difference between the date a plant began flowering minus 15 May, 1996 (the day before the first plant began flowering); 2) the distance of a plant to the nearest clone (a measure of isolation); 3) the number of fruit on a plant (to control for differential attraction of moths to plants). Then, I used multiple regression to determine if these same factors affected the cumulative number of droplets per plant, on those plants that had droplets at least once.

At the end of the season, 28 days after I had first seen droplets on each plant, I collected 1-2 fruit per yucca, and dissected them. I counted the number of non-pollinator oviposition scars on the inside of the fruit, the number of aprovechado larvae, and the number of intact versus damaged seeds per plant. I did this to determine if the day of flowering, isolation of a plant, or the number of fruit per plant had an affect on the presence or number of ovipositions per fruit, the presence or number of non-pollinator larvae per fruit, and the number of seeds destroyed. As above, I used logistic regression to determine if these factors influenced the presence or absence of ovipositions or larvae. Then, I used multiple regression in fruit with at least one oviposition scar, to determine if these factors affected the number of ovipositions or larvae per fruit.

Results

Longevity

Survival of non-pollinators differed depending on sex and whether the yucca had flowers and young fruit, or older fruit only. Average survival of females on plants with flowers (12 days) was higher than that of females on plants with fruit only (8 days; Log Rank = 27.12, d.f. = 1, $p < 0.0000$). Survival of males was also higher on plants with flowers (8 days) than plants without flowers (6 days; Log Rank = 7.01, d.f. = 1, $p = 0.008$; Figure 4.1).

Synchrony between Emergence and Yucca Flowering

Male non-pollinators emerged at the Yellow Jacket observation site in 1995 on 1 July, and females arrived on 7 July. In these six days, the floral/fruit environment changed drastically. When females emerged, there were 1/10th as many buds, ½ as many flowers, and 4 times as many maturing fruit than when males emerged (Figure 4.2). As well, in 1995, non-pollinators were not active much longer than the flowering season; there were flowers up until 5 days before the last day I saw droplets.

In 1996, the males emerged on the "fruit abortion" site at Old89 on June 9, and the females emerged on June 11. When females emerged, there were just over half as many buds, roughly the same number of flowers, and twice as many maturing fruit (Figure 4.3). Unlike in 1995, however, female non-pollinators were active on the site for 14 days after the last flowers were on the site.

To facilitate the comparison of 1995 with 1996, I compared the number of each type of flower/fruit to the number of plants per site (Figure 4.4). I found that in 1995, the males emerged slightly earlier in the yucca flowering season than they did in 1996. However, the females in 1995 emerged slightly later than in 1996, as there were more flowers and fruit per plant when the females emerged in 1996.

Spatial Experiment

The proportion of fruit with droplets per plant varied significantly between treatments (Figure 4.5). Control plants had a greater proportion of fruit with droplets than isolated plants ($F = 18.37$, d.f. = 1, $p<0.000$) and plants with older fruit had a greater proportion of fruit with droplets than did plants with younger fruit ($F = 34.65$, d.f. = 1, $p = 0.000$). There was also a significant interaction between fruit age and isolation of plants ($F = 8.2$, d.f = 1, $p = 0.004$); plants with older fruit received more droplets than those with young fruit and flowers when they were not isolated but there was no difference between the plants that were isolated, regardless of the presence of flowers on plants.

Oviposition counts confirmed the results of the above field observations on droplets (Figure 4.6). Again, control plants that were not isolated had more ovipositions per fruit than isolated plants ($H = 292.55$, d.f. = 1, $p < 0.001$), and early-flowering plants had more ovipositions per fruit than late-flowering plants. There was a significant interaction between the two factors; the number of ovipositions did not differ between early and late-flowering plants that were isolated, but there was a difference between early and late-flowering plants that were not isolated.

Spatial Observations

The proportion of nights that individual plants had droplets increased slightly with the date of plant flowering ($p = 0.001$, $\beta = 0.21$, $t = 3.49$) and the number of fruit ($p = 0.000$, $\beta = 0.305$, $t = 5.06$, $p < 0.000$; model $r^2 = 0.12$, d.f = 253) but was not affected by a plant's distance to the nearest clone (Figure 4.7). However, only the number of fruit per plant affected the cumulative number of droplets per plant on plants that did have droplets ($r^2 = 0.26$, d,f, = 189, $\beta = 0.51$, $t = 7.91$, $p < 0.000$).

The probability that a fruit had non-pollinator oviposition scars was influenced by both the number of fruit per plant, and the date of plant flowering, but not by distance to nearest neighbour (Table 4.1). Fruit were more likely to have ovipositions, as the number of fruit per plant increased, but the presence of ovipositions in fruit did not increase linearly with the date of flowering. Instead, it increased with the date of flowering initially, but then decreased. However, the number of ovipositions per fruit increased linearly with flowering date (Table 4.2).

Finally, I found no relationship between a plants' number of fruit, date of flowering, and isolation on the presence (n = 359) or number of non-pollinator larvae in fruit (d.f. = 358, $r^2 = 0.000$).

Discussion

In this chapter, I examine how the population structure of yuccas, and the life-history synchronization between non-pollinators and yuccas, affect non-pollinator oviposition activity. In both years, non-pollinator emergence was well synchronized with yucca flowering, as female non-pollinators emerged just as fruit 7 days and older were maturing on the sites. Even though non-pollinator emergence and yucca fruiting were well timed, synchrony between non-pollinators and yuccas is probably not as critical as I first predicted, because the moths can live without yucca flowers, and live much longer than expected. I found that the population structure of mutualists can have a strong effect on which yuccas are parasitized. Generally, plants isolated in space are rarely used, regardless of fruit age, but on plants that are not isolated, those with older fruit get used more often. However, this isolation must be very high (>100m) before there is a significant decrease in the number of ovipositions per fruit. Depending on the timing of non-pollinator emergence, though, some plants can be considered to be isolated in time, as plants with very young fruit in 1995 were rarely used by non-pollinators. Together, synchronization of life-histories and particularly the distribution of yuccas in space, may alter non-pollinator oviposition activity and protect some yuccas from being exploited.

Earlier, I proposed that a factor that could severely limit non-pollinator population growth (and therefore exploitation of yuccas) was the asynchrony of non-pollinator emergence and the yucca flowering season. I suggested this for several reasons. First, unlike other parasites of plant-pollinator systems, such as nectar robbers, non-pollinators are obligately dependent on yuccas and therefore do not have the opportunity of exploiting other resources if they emerge asynchronously with yucca flowering and fruiting. Second, unlike the exploiters of the fig-fig wasp mutualism which are also obligately dependent on their hosts (Kerdelhue and Rasplus 1996; West and Herre 1994), yucca fruit are not available all year around, so timing should be critical; the longevity of the moth, coupled with the state of the yucca flowering season when the non-pollinators emerge, should determine how successful non-pollinators are in a given year. Third, I originally thought flowers were critical for non-pollinator survivorship, and while they do appear to improve longevity, they are not essential.

I found that asynchrony of life histories did not present a problem for non-pollinators in either season. In both 1995 and 1996 I found that non-pollinators emerged just as fruit greater than 6 days old were available, and while there still were flowers to mate and rest in. Based on my previous assumptions, this would be the "Correct" time for non-pollinators to emerge. However, only halfway into the 1996 non-pollinator season, there were no longer any flowers on the observation site, and the moths continued to oviposit into fruit for two weeks. This suggests that the presence of flowers is not critical to non-pollinator survival and mating. In fact, based on this study, I suggest that asynchrony generally is not a problem for non-pollinators, for the following four reasons.

First, non-pollinator's relatively long life span helps them "wait out the yuccas" if they emerge early in the season. The females lived an average of 12 days on plants with flowers and fruit, and 8 days on plants without flowers, and (as seen in Figure 4.1) yucca flowering and fruiting can change immensely in just 6 days.

Second, asynchrony may not severely reduce the fitness of individual moths if their progeny emerge over a period of several weeks. Even if the first moths emerge too early, and they cannot live until fruit are available, other moths may emerge a week or even two weeks later, and can exploit fruit at this time. This may be a mechanism for moths to spread the risk of having all of their young emerge at once, but not synchronized with yucca fruit production. Yucca flowering and fruiting is very sensitive to yearly fluctuations in temperature and rainfall. For example, in our sites, flowering began on 6 June in 1995 and on 11 May in 1996. If all of a moth's offspring emerged at the same time, and there were no fruit available, its fitness would be severely diminished. However, if the offspring of that same moth emerged over a period of several weeks, there is a greater chance that at least some of the young will find suitable fruit. This risk-spreading strategy is somewhat analogous to systems (including this one) in which insects have prolonged diapause (Wipking 1990; Menu and Debouzie 1993; Powell 1989; Fuller 1990; Reviewed in Hanski 1988). Here, the young of a cohort emerge in different years to help wait out the "bad years" and capitalize on the good.

Third, asynchrony of life-histories may not be a problem for non-pollinators if they have some mechanism for determining when yucca flowering is at its peak (when the first fruit are just beginning to mature) and emerging at this time. In both seasons, non-pollinators emerged at, or just after peak yucca flowering, despite the fact that flowering occurred at different times in both years. This suggests that the larvae can detect environmental cues, even though they are 10-20 cm under the soil in diapause (Fuller 1990), which stimulate them to pupate and emerge "on time". On a crude scale, it is possible that precipitation may stimulate more non-pollinators to emerge in a given year, as has been shown with *Tegeticula yuccasella* (Fuller 1990) On a finer scale, however, the cue(s) for stimulating the emergence of moths in a given three-week period within the season are not fully understood, although in other systems temperature has been suggested as a possible cue (Battisti 1994).

Fourth, asynchrony of life-histories may not be a problem if non-pollinators emerge late in the yucca's flowering season, because although they do not oviposit in fruit younger than 8 days old, they lay eggs in fruit up to 30 days old. This gives them great flexibility, particularly if they emerge later in the season. The probability of encountering fruit in this age range is very high.

Population Structure of Yuccas

In several systems, the population structure of hosts can influence the behaviour and use by parasites (Louda 1982; Biere and Honders 1996). For example, parasites may prefer to target hosts of a particular age because those hosts provide the most reward (Biere and Honders 1996; Dodds et. al. 1996; Hoddle 1991). Alternatively (or additionally) the distribution of hosts may influence parasite behaviour. For instance, parasites, like mutualists, may benefit most where hosts are the most abundant, because the cost of searching for them is reduced (Sih and Baltus 1987, Aagren 1996).

In my spatial experiment, I found that the age of fruit and the distance of plants from their nearest neighbour strongly affected the extent to which yucca fruit were exploited by non-pollinators. Moths used older fruit on non-isolated plants much more than they used either plants at high density with young fruit and flowers, or isolated plants with fruit of any age.

Originally, I predicted that isolated plants with flowers and fruit would get hit especially hard, because they would attract non-pollinators from a wide area for resting and mating. Then, since there were no other yuccas nearby, the moths would stay and oviposit in them as well. However, I have found three reasons why this should not occur. First, non-pollinators avoid very young fruit, and should not exploit isolated plants with young fruit, even if these plants have flowers to rest in. Second, they tend to oviposit in the fruit of one plant very heavily, and then fly far away to another clone (personal observations), in a similar manner to yucca moths (Aker and Udovic 1981). Because there are no yuccas near by to keep these moths in the "neighborhood", they may keep flying until they reach another plant, more than 100 m away; the chances of this moth returning to this plant, then, are very slim. Third, moths do not need flowers to rest and mate, so they may not be especially attracted to these plants in the first place.

The results of the spatial observations in 1996 did not support the spatial experiment. In the observation study, I found that the presence and number of droplets was affected by the date that plants began flowering. Instead of strictly choosing to oviposit in older fruit, however, the droplets data suggest that the moths oviposited more often in plants with younger fruit, while the oviposition data suggest that moths chose to oviposit in fruit of middle age more often, but once they did choose to lay eggs in fruit, they did so more heavily in the younger ones. On the surface, these data suggest that moths are making different fruit choices in different years. However, I do not believe that this is the case. The answer to the difference in the ages of fruit chosen in different years, lies in the age of fruit available to the moths. In 1995, despite what the Snapshot data suggest, female moths were out relatively earlier with respect to yucca flowering.

Flowers were available on the "Yellow Jacket" observation site until 5 days before the end of the non-pollinator flight season. The fruit available to them were therefore fairly young. Since moths tend to oviposit in fruit of middle ages (from 8 to 30 days old), they appeared to be selecting older fruit in 1995. In 1996, female non-pollinators were on the observation site for two weeks after the last flowers were abscised. Indeed, by the end of the non-pollinator flight season, some of the fruit on the "Old 89" site were up to 48 days old, far older than the oldest fruit these non-pollinators have been seen to lay eggs in (personal observations, Addicott in prep.). Consequently, the fruit available to non-pollinators were older in 1996 than in 1995, and because the moths oviposit in fruit of "middle age", they appeared to be selecting younger fruit.

The oviposition data demonstrate this pattern of choosing middle aged fruit more clearly. Data on ovipositions per fruit do not provide an indication of the pattern of non-pollinator oviposition activity on a nightly basis as droplets can, but provide a much more quantitative picture of the cumulative affects of non-pollinator activity than an analysis of the cumulative number of droplets per plant. The probability that a fruit had oviposition scars was described by a quadratic function that increased initially with the date of flowering, but then decreased, suggesting that moths avoided fruit at either extreme. However, in 1996, the number of ovipositions per fruit, once it had ovipositions, increased linearly with the date of flowering, suggesting that if a younger fruit was old enough to be oviposited into, it was hit quite hard. I was not expecting this, based on analyses (see Chapters 2 and 3) that suggest that non-pollinator survival increased in older fruit, and at present cannot explain this pattern.

In my observation study, I found no effect of yucca isolation on the presence or cumulative number of droplets on plants. The reason why plant isolation did not strongly influence non-pollinator oviposition activity on a given night was probably because my site was primarily a high density site compared to the spatial experiment. The average distance of clones from one another was 15 meters, and the furthest distance between two clones was 74 meters. I expect that if I had chosen a site with the extremes of isolation that I had in the spatial experiment, I would have seen an effect of isolation in this site as well.

The focus of this chapter was to determine if yuccas that are isolated in time and space can escape exploitation by non-pollinators. My studies of non-pollinator emergence, and oviposition activity in the fruit of plants at different densities and flowering times suggests that indeed some plants can escape non-pollinator ovipositions. The escape in space, however, requires very high isolation, isolation that does not exist at our study site, except for perhaps a few isolated plants. The escape in time depends strongly on the timing of non-pollinator emergence with respect to yucca flowering, and given that moth emergence with respect to yucca flowering changes from year to year, the escape in time is a stochastic one. However, a study on non-pollinator oviposition activity tests only the potential for non-pollinators to exploit different plants. In 1996, while I found a consistent pattern of date of flowering influencing oviposition activity, I found that none of the variables (flowering time, isolation, number of fruit) influenced the presence and number of non-pollinators in fruit. This is likely due to strong interspecific competition from pollinating larvae, which may destroy any pattern of non-pollinator exploitation that might be created through non-pollinator fruit choice.

Literature Cited

Aagren, J. 1996. Population size, pollinator limitation, and seed-set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77, no. 6: 1779-90.

Ackerman, J. D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. *Biological Journal of the Linnean Society* 20, no. 3: 301-14.

Addicott, J. F. 1986. Variation in the costs and benefits of mutualism: The interaction between yuccas and yucca moths. *Oecologia* 70, no. 486-494.

———. 1996. Cheaters in yucca/moth mutualism. *Nature (London)* 380: 114-15.

Addicott, J. F. and A. J. Tyre. 1995. Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72: 382-94.

Addicott, J. F., J. Bronstein, and F. Kjellberg. 1990. Evolution of Mutualistic Life-Cycles: Yucca Moths and Fig Wasps. *Insect Life Cycles.* 1 ed., Editor Francis Gilbert, 143-61. London: Springer-Verlag.

Aker, C. L. and D. Udovic. 1981. Oviposition and pollination behaviour of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49: 96-101.

Battisti, A. 1994. Voltinism and diapause in the spruce web-spinning sawfly *Cephalcia arvensis*. *Entomol. Exp. Appl.* 70, no. 2: 105-13.

Biere, A. and S. J. Honders. 1996. Impact of flowering phenology of Silene alba and S. dioica on susceptibility to fungal infection and seed predation. *Oikos* 77, no. 3: 467-80.

Bradshaw, W. E. 1990. The present and future of insect life-cycle evolution. *Insect Life Cycles: Genetics, Evolution and Coordination.* editor F. Gilbert, 243-51. London, UK: Springer-Verlag.

Breton, L. M. and J. F. Addicott. 1992. Density-dependent mutualism in an aphid-ant interaction. *Ecology* 73, no. 6: 2175-80.

Copland, B. J. and R. J. Whelan. 1989. Seasonal variation in flowering intensity and pollination limitation of fruit set in four co-occurring *Bansksia* species. *Journal of Ecology* 77, no. 2: 509-28.

Dodds, K. A., K. Clancy, K.J. Levya, D. Greenberg, and P. W. Price. 1996. Effects of Douglas-fir foliage age class on western spruce budworm oviposition choice and larval performance. *Great Basin Naturalist* 56, no. 2: 135-41.

Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton, New Jersey: Princeton University Press.

Fuller, O. S. 1990. "Factors affecting the balance of cooperation and conflict between the yucca moth, *Tegeticula yuccasella* and its mutualist, *Yucca glauca*." University of New Mexico.

Halley, J. M. and J. P. Dempster. 1996. The spatial population dynamics of insects exploiting a patchy food resource: A model study of local persistence. *Journal of Applied Ecology* 33, no. 3: 439-54.

Hanski, I. 1988. Four kinds of extra long diapause in insects: A review of theory and observations. *Annales Zoologici Fennici* 25, no. 1: 37-53.

Herrera, C. M. 1990. Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos* 58: 277-88.

Hoddle, M. S. 1991. Gorse pod susceptibility and oviposition preference to the gorse seed weevil, *Apion ulicis* (Forster) (Coleoptera:Apionidae). *New Zealand Journal of Zoology* 18, no. 1: 31-35.

House, S. M. 1993. Pollination success in a population of dioecious rain forest trees. *Oecologia* 96, no. 4: 555-61.

Howe, H. F. 1984. Constraints on the evolution of mutualism. *The American Naturalist* 123, no. 6: 764-77.

Keeley, J. E., C.S. Keeley and D. A Ikeda. 1986. Seed predation by yucca moths on semelparous, iteroparous and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). *The American Midland Naturalist* 115, no. 1: 1-9.

Kerdelhue, C. and J. Rasplus. 1996. Non-pollinating Afrotropical fig wasps affect fig-pollinator mutualism in *Ficus* within the subgenus Sycomorus. *Oikos* 75: 3-14.

Levine, S. H. and R. E. Wetzler. 1996. Modelling the role of host plant dispersion in the search success of herbivorous insects: Implications for ecological pest management. *Ecological Modelling* 89: 183-96.

Louda, M. 1982. Inflorescence spiders: A cost-benefit analysis for the host plant *Haplopappus venetus* Blake (Asreraceae). *Oecologia* 55: 185-91.

McKey, D. 1989. Population biology of figs: Applications for conservation. *Experentia* 45, no. 7: 661-73.

Menu, F. and D. Debouzie. 1993. Coin-flipping plasticity and prolonged diapause in insects: Example of the chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae). *Oecologia* 93, no. 3: 367-73.

Miller, G. E. and D. S. Ruth. 1986. Effect of temperature during May to August on termination of prolonged diapause in the Douglas-fir cone moth

(Lepidoptera:Tortricidae). *Canadian Entomologist* 118, no. 10: 1073-74.

Murphy E.C. and J.H. Schauer. 1996. Synchrony in egg-laying and reproductive success of neighbouring common murres, *Uria aalgae* . *Behavioural Ecology and Sociobiology* 39, no. 4: 245-58.

Parker, G. A. and R. A. Stuart. 1976. Animal behaviour as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *The American Naturalist* 110: 1055-76.

Parker, G. A. and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behavior* 34: 1222-42.

Pellmyr, O., J., Leebens-Mack, and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-56.

Powell, J. A. 1989. Synchronized, mass-emergences of a yucca moth, *Prodoxus y-inversus* (Lepidoptera:Prodoxidae), after 16 and 17 years in diapause. *Oecologia* 81, no. 4: 490-493.

Powell, J. A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7, no. 1: 10-14.

Riley, C. V. 1892. The yucca moth and yucca pollination. *Annual Report of the Missouri Botanical Garden* 3: 99-159.

Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63, no. 2: 354-60.

Schemske, D. W. 1983. Limits to specialization and coevolution in plant-animal mutualisms. *Coevolution.* editor M. H. Nitecki, 67-111. Chicago, USA: University of Chicago Press.

Sih, A. and M. S. Baltus. 1987. Patch size, pollinator behaviour, and pollination limitation in catnip. *Ecology* 68, no. 6: 1679-90.

Smith-Ramirez, C. and J. J. Armesto. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloe, Chile - Ecologies and climatic constraints. *Journal of Ecology* 82, no. 2: 353-65.

Soberon Mainero, J. and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic systems. *The Biology of Mutualism.* editor D. H. Boucher, 192-216. London: Croom Helm.

Solbreck, C., D.B. Anderson, and J. Forare. 1990. Migration and the coordination of life-cycles as exemplified by Lygaeinae bugs. *Insect Life Cycles: Genetics, Evolution and Co-ordination.* editor F. Gilbert, 197-214. London, UK: Springer-Verlag.

Subramanya S. and T.R. Radhamani. 1993. Pollination by bats and birds. *Current Science* 65, no. 3: 201-9.

West, S. A. and E. A. Herre. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London B.* 258: 67-72.

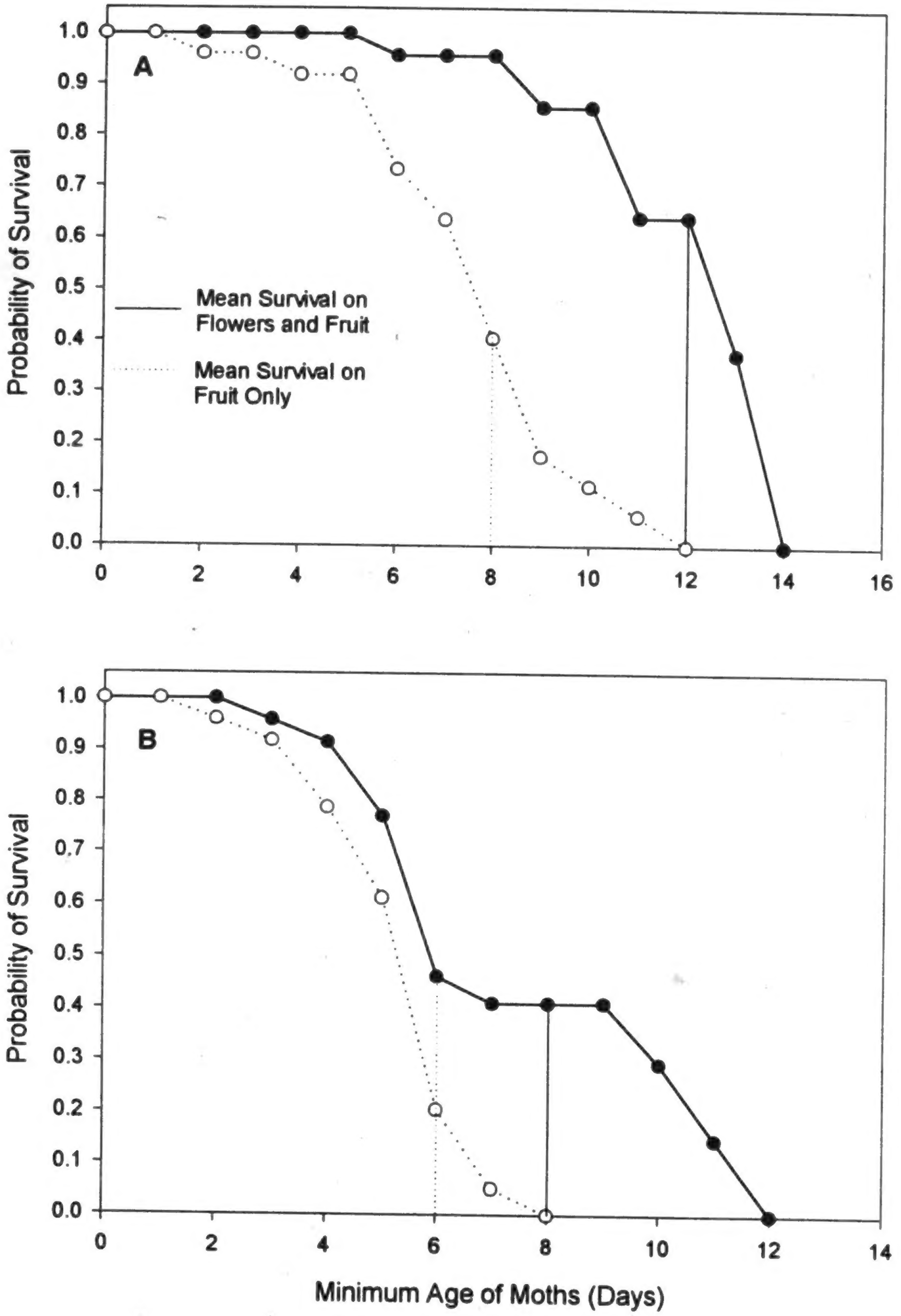

Figure 4.1: Survival of A) female and B) male non-pollinators on plants with flowers and fruit or just fruit.

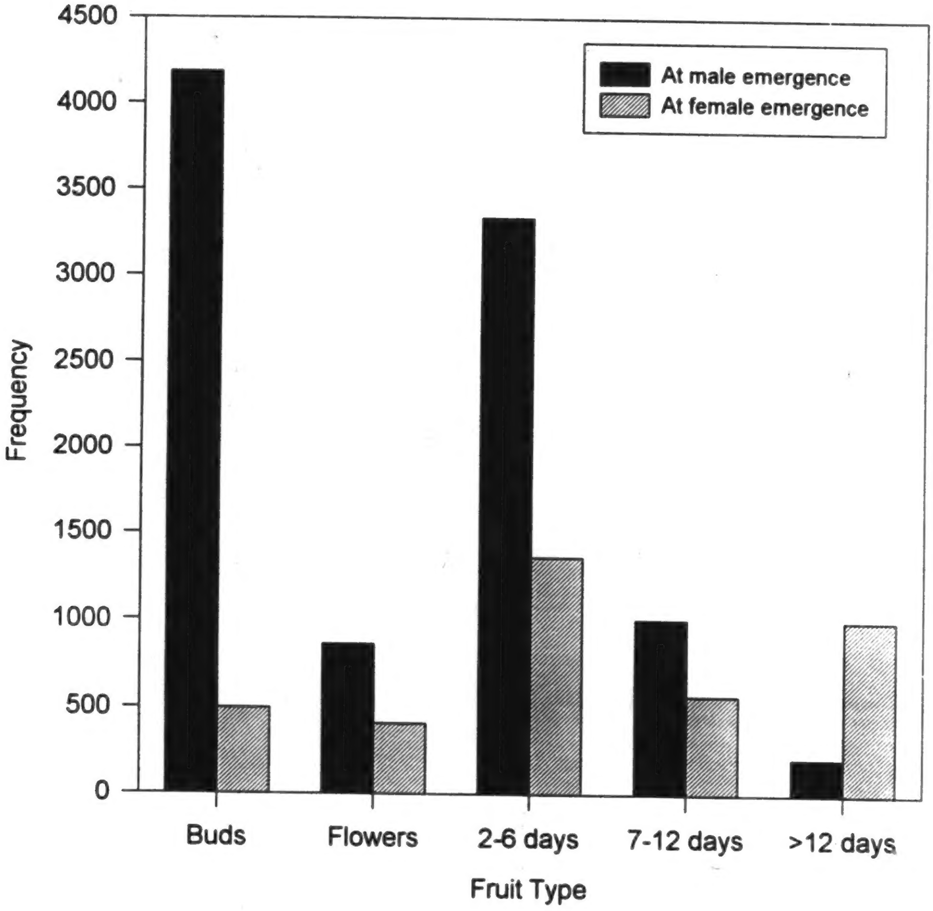

Figure 4.2: Number of buds, flowers and fruit of different ages in 1995 when male and female non-pollinator moths emerged.

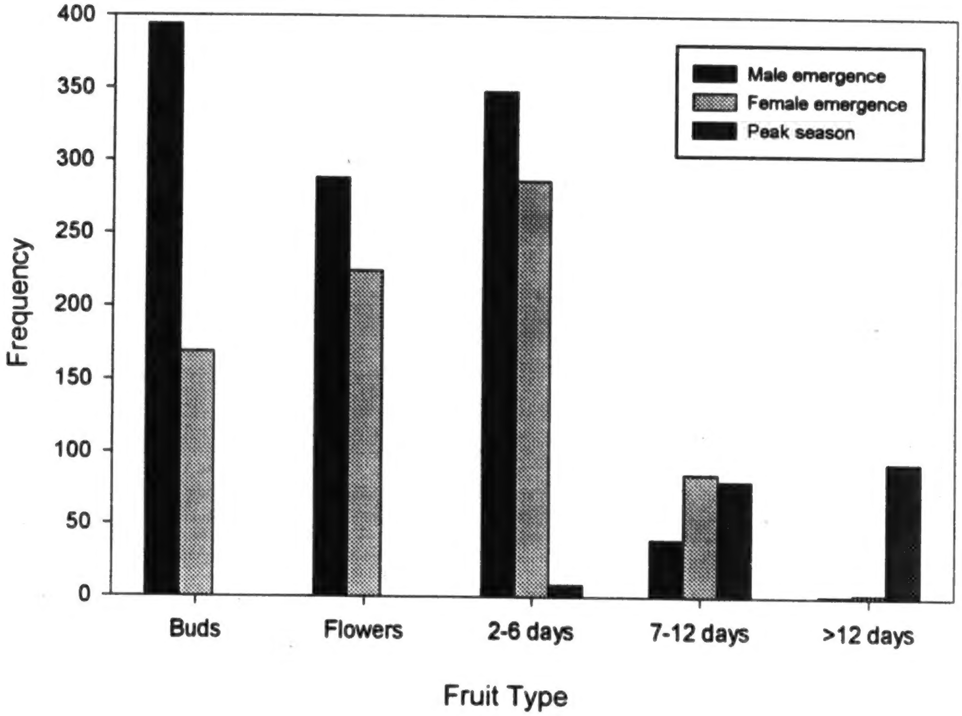

Figure 4.3: A comparison of the numbers of buds, flowers and fruit of different ages on 20 yucca plants at different times during the 1996 non-pollinator flight season.

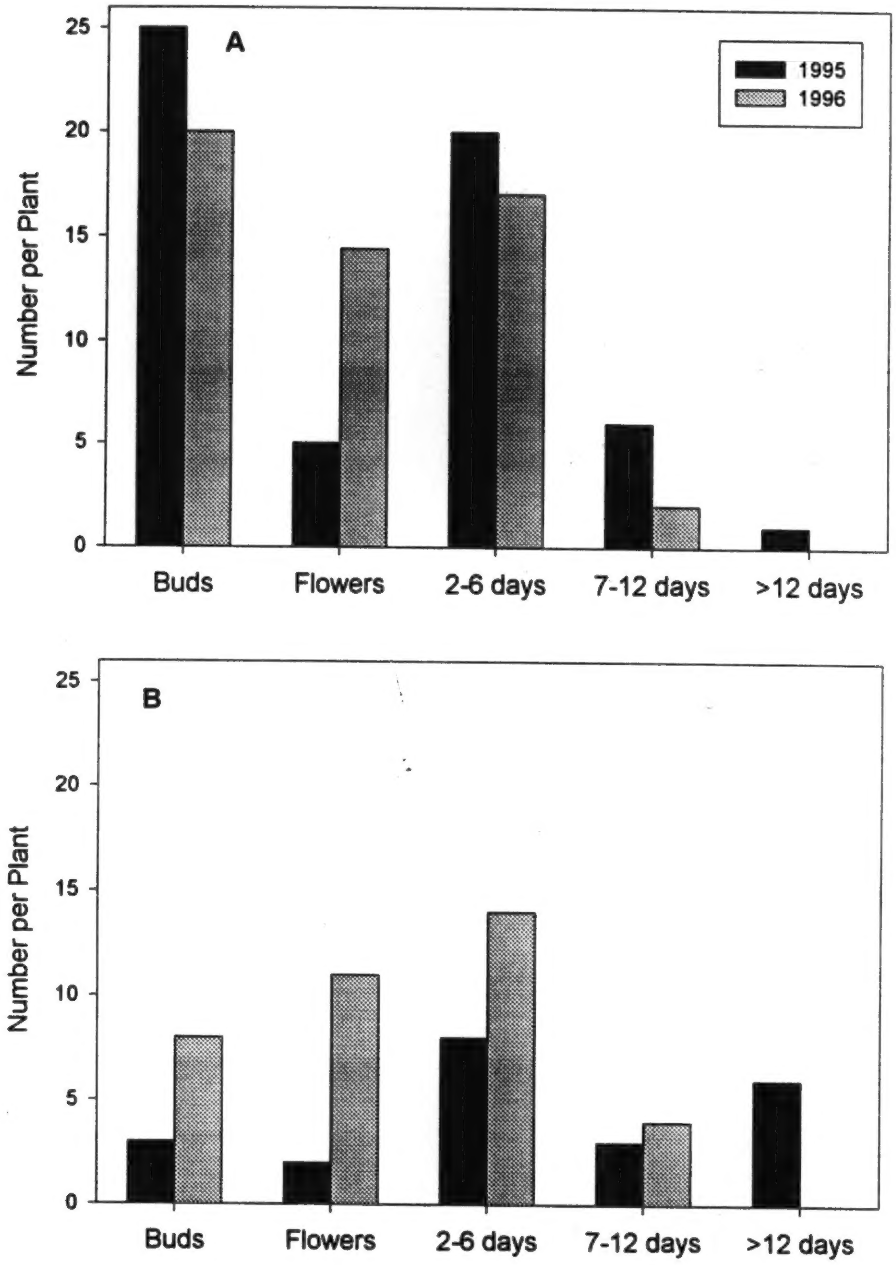

Figure 4.4: A) The average number of buds, flowers and fruit of different ages when non-pollinators emerged in both years. A) At male emergence B) At female emergence.

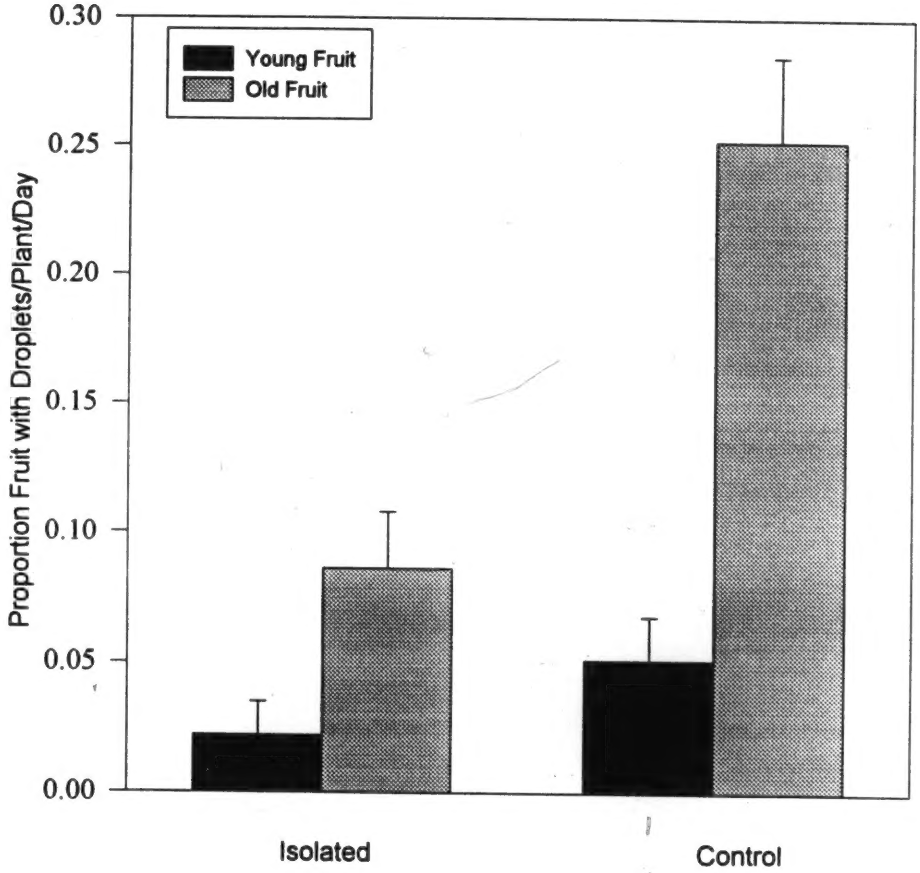

Figure 4.5: Proportion of fruit with droplets per plant per day on isolated plants and non-isolated plants, with either young fruit < 12 days, and old fruit > 12 days old.

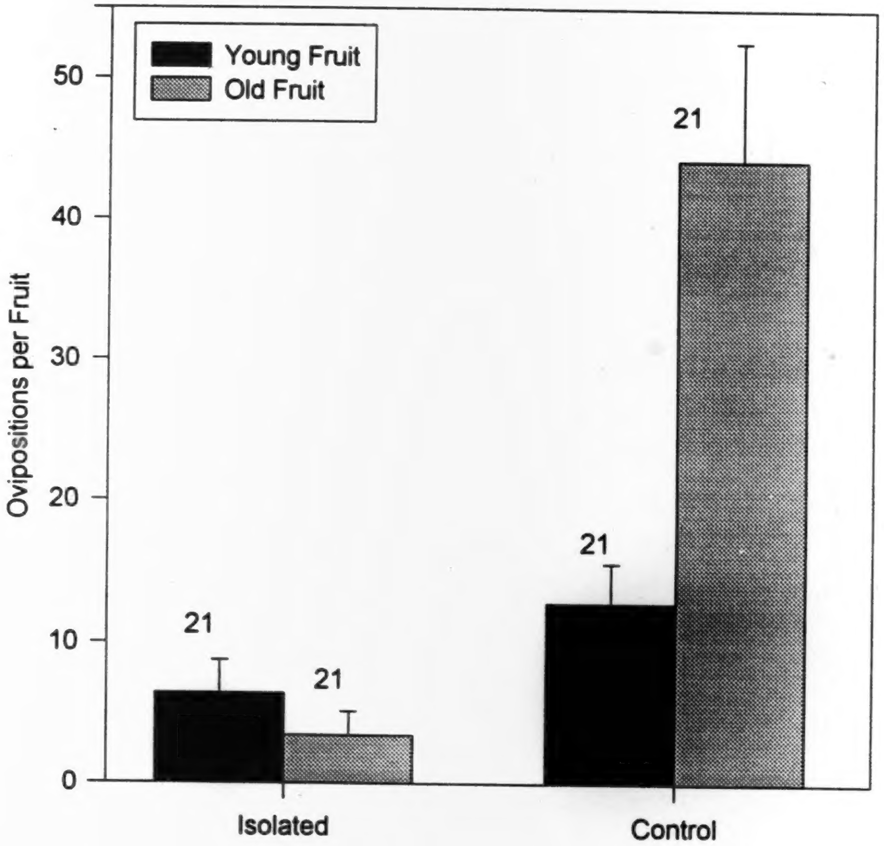

Figure 4.6: Ovipositions per fruit on plants that were isolated, or not isolated, with young fruit and flowers < 12 days old, and old fruit > 12 days old.

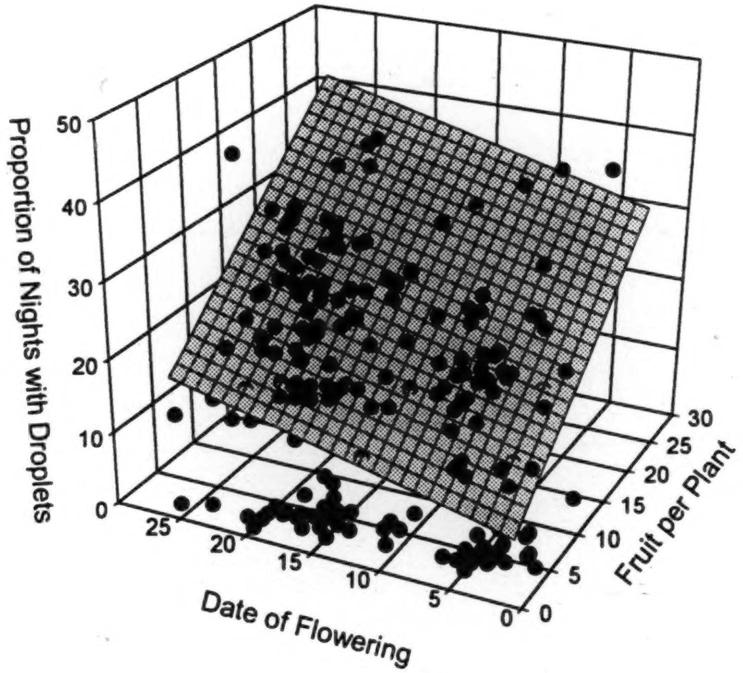

Figure 4.7: Proportion of nights that a plant has droplets out of the nights available (arc sine square root transformed) versus the number of fruit per plant, and the date - May 15, 1996 that the plant began flowering. Surface plot represents the proportion of nights with droplets as predicted by multiple linear regression. Symbols represent the proportion of nights a plant is seen with droplets. y = 5.97 + (0.43*Date Flowering) + (1.13*Number of Fruit).

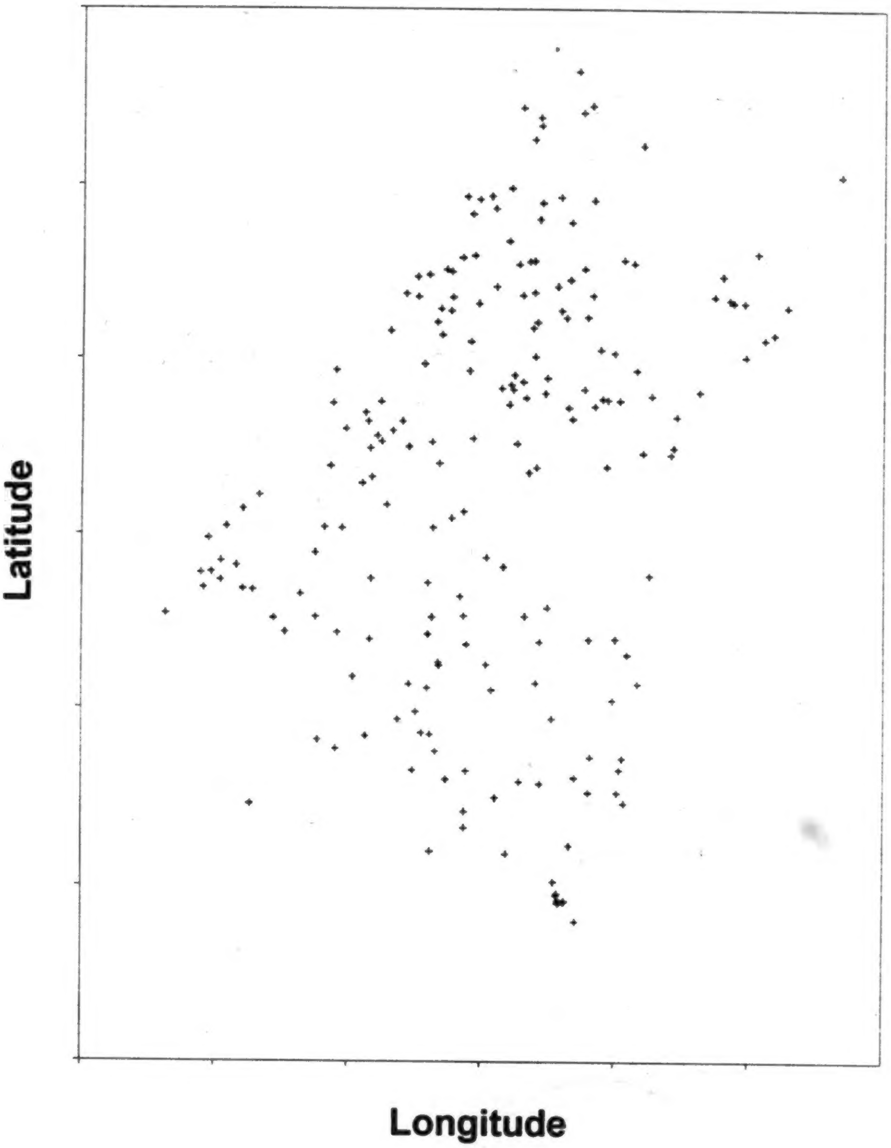
Latitude
Longitude

Figure 4.8: Map of 1996 "Old 89" spatial observation site. Symbols represent yucca clones, within which there were blooming plants.

Table 4.1: The results of logistic regression analysis on the factors affecting the presence or absence of non-pollinator oviposition scars in fruit.

Variable	B	Wald	Significance	R
Date Plant Began Flowering	0.394	7.37	0.007	0.163
(Date Plant Began Flowering)^2	-0.013	3.58	0.059	0.089
Number of Fruit on Plant	0.153	3.78	0.052	0.094
Constant	-7.17	0.80	0.372	

Table 4.2: Results of multiple regression analysis on the factors influencing the number of ovipositions in fruit.

Variable	B	t	p
Date Plant Began Flowering	1.05	3.52	< 0.000
Constant	22.37	5.73	< 0.000

Chapter 5

Summary

Overview

Many mutualisms are exploited by organisms which benefit from mutualistic resources or services, but do not reciprocate (Soberon and Martinez 1985). In some cases, the exploiter has a commensal relationship with its hosts, reaping benefits without noticeably harming the mutualists (Bronstein 1991; Morris 1996). In others, the exploiter is clearly a parasite, and reduces the survivorship or reproduction of its hosts (Roubik 1982; Roubik et. al. 1985; Bultman and Mathews 1996; Letourneau 1990 and 1991). In systems where the exploiters are most damaging, the mutualists may be faced with one of two outcomes. First, the mutualism may collapse. If this occurs, and the mutualism was obligate, the mutualists may go extinct. If the mutualism is facultative, the mutualists may shift to a mode of life that does not require mutualism, or may simply rely on other mutualists. Second, the mutualism does not collapse because there are processes that limit the impact of the exploiter on the mutualism so that at least for some of them, the impact is reduced.

For my M.Sc. thesis, I addressed three processes that limit exploitation. First, mutualists may develop chemical, morphological, or behavioural traits to either prevent intrusion by exploiters, or eliminate them once they do invade (Inouye 1983; Janzen 1975; Stevenson 1981, 1982; Prys-Jones and Willmer 1992). Second, exploiters themselves may regulate their impact on mutualists through density-dependent mechanisms, such as intraspecific competition for mutualistic resources (Alexandersson and Aagren 1996). Finally, exploitation of some mutualists may be limited through escape in time and space. For instance, on a large scale, processes that promote asynchrony of the life cycles of exploiters and its mutualists may limit exploitation, since exploiters simply will not encounter mutualists (Louda 1982; Biere and Honders 1996). On a smaller scale, differences in the ages and distribution of mutualists increase the risk that some mutualists will be exploited, but allow others to escape completely.

I examined these three limits to the exploitation of the mutualism between *Yucca kanabensis* and *Tegeticula yuccasella* spp. by an unnamed non-pollinating moth. All three of these factors could potentially play a role in this system for several reasons. First, non-pollinators lay eggs in the same yucca fruit that pollinating moths do (Addicott et. al. 1990; Addicott 1996; Pellmyr 1996). And since yuccas are known to selectively abscise flowers with high numbers of pollinator ovipositions (Addicott 1998; Pellmyr and Huth 1994; Richter and Weiss 1995) , they might also be able to selectively abort yucca fruit with high numbers of non-pollinator ovipositions. Second, yucca fruit are restricted environments in which non-pollinator larvae could experience interspecific competition from pollinator larvae and intraspecific competition among themselves. Third, non-pollinators are also obligately dependent on yucca fruit, which are available only once a year because yucca blooming is seasonal. Therefore, it is critical that the non-pollinator life cycle be synchronized with that of yucca fruiting and pollinator activity, or they will not have fruit to oviposit in and could suffer massive population declines. Fourth, non-pollinators should take advantage of yuccas at high density because there is less travel time and risk of predation when flying to nearby plants than when flying to isolated plants. Since yucca density varies widely over the space of several kilometers, some isolated yuccas may be at lower risk of exploitation than others.

Major Findings and Future Work

Limits to Exploitation by the Yucca and the Yucca moth

In this system, only one of the mutualists, the pollinating moths, plays a role in limiting exploitation by the non-pollinator. The pollinators do this through strong interspecific competition between larvae in the fruit (Chapter 2). The yuccas, on the other hand, were not able to regulate non-pollinator numbers through fruit abortion. In fact, yuccas actually retained fruit with more non-pollinator droplets on them, probably because non-pollinators tend to oviposit in older fruit that are less likely to be abscised.

The competition between non-pollinators and pollinator larvae was more severe at the Old 89 site where survival of non-pollinators was significantly lower, and the density of pollinator larvae per fruit was significantly higher than at the Yellow Jacket site (Chapter 2). At the Old 89 site, there are two pollinating moths, "shallows" and "deeps" (Tyre and Addicott 1993; Wilson and Addicott 1998). The shallows can reach very high numbers in fruit (>40) because the plant does not selectively abscise flowers with high numbers of ovipositions of these moths. At the Yellow Jacket site, only "deep" pollinators are found, which are regulated by yucca flower abscission. It is possible that non-pollinators may be competitively excluded through competition by the "shallows" at Old 89, but that they may be able to persist at Yellow Jacket, where competition is less prevalent.

The concepts of competitive exclusion and coexistence between the different species of moths associated with yucca flowers and fruit is a rich area for further study. First, more detailed comparisons of non-pollinator reproductive success and population densities at the two sites are required to determine if they are suffering stronger competition at Old 89, as my data are just preliminary. Second, the non-pollinators could be included in a model of yucca moth coexistence and competitive exclusion (Csotonyi and Addicott, unpublished) to determine the conditions under which we should expect non-pollinators to coexist with the "shallows" or be excluded by them.

Limits to Exploitation by the Non-pollinator

Intraspecific competition between non-pollinator larvae in fruit did occur, but it was neither as prevalent nor as intense interspecific competition (Chapter 3), and probably does not play a strong role in limiting non-pollinator numbers or non-pollinator exploitation. As expected, noticeable decreases in non-pollinator survival did not occur until the larvae reached fourth instar, at which time they began to consume large numbers of seeds, and interfere with the feeding of other larvae in a locule.

When I examined non-pollinator oviposition activity for evidence that non-pollinators spread their ovipositions to avoid intraspecific competition, I found ovipositions to be highly aggregated in space. This suggests that rather than trying to avoid intraspecific competition, non-pollinating moths are using fruit efficiently, and minimizing flight and search time between plants. It is possible that the moths do this because intraspecific competition is not a large cause of mortality, and that the egg load of a single female is unlikely to result in so many larvae that they compete for seeds. On the other hand, an analysis of the number of times droplets were seen on a given fruit suggests that fewer fruit had no droplets than would be expected by chance, and more fruit had droplets only once than expected by chance. This seems to suggest that non-pollinators might recognize which fruit have been hit previously by non-pollinators, possibly by cueing in on droplets. However, this result was only marginally significant, and could also be explained by the simple fact that as the season progresses, yucca fruit get older, shifting the fruit that are available to non-pollinating moths. For example, fruit that were 25 days old at the beginning of the non-pollinator flight season, would be 35 days old at the peak of the season, and no longer attractive to non-pollinating moths.

My work in examining non-pollinator oviposition activity is preliminary, and this is another area that deserves attention in the future. As I discussed in Chapter 3, oviposition by insects is analogous to optimal foraging problems in which there are tradeoffs between the energy expended to locate patches (in this case, fruit) and potential fitness losses due to competition between offspring in those patches. The situation is even further complicated when more than one female can oviposit in a patch (Ives 1989; Parker and Begon 1986; Holmes 1972; Ives 1989; Skinner and Mandracchia 1985). In the yucca-yucca moth system more than one female non-pollinator can oviposit in a fruit, which has already been oviposited in by one or more female pollinating moths. Theory suggests that non-pollinators should spread out ovipositions more in fruit where there is strong competition Old 89 (Ives 1989; Parker and Begon 1986; Holmes 1972 but see Ives 1989; Skinner 1985), and aggregate ovipositions more where competition is weaker - Yellow Jacket. An excellent study could be performed to determine if non-pollinator activity obeys the "rules" of optimal oviposition theory, and is different in the two sites. My preliminary studies show that the number of ovipositions per fruit or per locule are significantly lower at Old 89 than at Yellow Jacket, and that in both cases, on *average*, the number of larvae per fruit tends not to exceed the carrying capacity of the fruit. However, at each site, there does not appear to be a relationship between the number of pollinator larvae per fruit and the number of non-pollinator ovipositions (Chapter 3 -

discussion). Therefore, the differences in ovipositions between the sites could be site-specific, rather than plant or fruit-specific, meaning that non-pollinators may oviposit differently at the two sites because on average they will encounter fruit with more or fewer pollinators. On the other hand, the differences could simply be due to differences in moth densities in the two areas.

Escape of Mutualists in Time and Space

a) Synchrony of Non-pollinator and Mutualist's Life Histories

The emergence of non-pollinators was very well timed with the appearance of yucca fruit in 1995 and 1996 (Chapter 4), so asynchrony did not pose a problem for non-pollinators during this study. However, even if they emerged relatively early in the flowering season, females lived an average of 12 days on plants with flowers, and could probably emerge even before yuccas began flowering, and still have an opportunity to oviposit. Likewise, if they emerge relatively late, they would not likely be excluded from ovipositing in fruit, because they can oviposit in fruit up to 30 days old.

The timing of non-pollinator emergence was good in 1995 and 1996, despite the fact that there was an almost 4 week difference between the date of first blossom in those two years. This is not always the case, as in 1994, non-pollinators either did not emerge, or emerged very late in the season after all of the flowers were gone (Wilson and Addicott unpublished results). But, on the whole, it suggests that the moths can perceive some environmental cue that triggers emergence.

Previous studies suggest that moisture and temperature regimes may play a role in triggering a larger number of yucca moths to emerge in a given year (Fuller 1990; Powell 1989), but no work has been done to determine why moths emerge at a precise time within a year. To further complicate the matter, pollinators and non-pollinators probably use the same cues, based on their very similar biology, yet they respond to them differently, with non-pollinators emerging 2-3 weeks later than pollinators in any given year. How they accomplish this is unknown.

b) Population Structure of Yuccas

In the 1995 spatial experiment, I found large differences in non-pollinator use of plants that were either isolated or not isolated, that had old fruit and young fruit. The fruit on isolated plants (100m from the nearest yucca with flowers or fruit) had very little non-pollinator use. As well, plants at high density sites with very young fruit were hit almost as little as isolated ones, while plants at high density with older fruit were heavily hit. The results of the spatial observations in 1996 differed from 1995. In this study, non-pollinators oviposited in the younger and "middle aged" fruit more often, and there was no effect of distance. However, I suspect the lack of an isolation effect was due to the choice of study site which contained very few isolated plants - and none as isolated as those in the experiment.

Conclusions

In the yucca-yucca moth mutualism, exploitation by the non-pollinator can be severe. In 1995 and 1996, over 90% of yucca fruit had non-pollinator ovipositions, and yuccas lost an average of 30% of their seeds to non-pollinator seed consumption. Further, non-pollinators oviposit in fruit after the abscission decisions of the plant are made, and are not subject to regulation by the yucca in the way some pollinating moths are.

In this system, intraspecific competition between non-pollinators plays only a small role. Indeed there appears to have been no selection for non-pollinator moths to avoid intraspecific competition by spreading their ovipositions among fruit, as ovipositions are highly aggregated in space.

Likewise, one of the strongest potential limits to exploitation, asynchrony of non-pollinator and mutualist life cycles, also appears to play a limited role. Asynchrony could limit exploitation because extremely early or late non-pollinator emergence would place them in an environment with no fruit, and no opportunity for reproduction, with disastrous consequences to the moths. But moth emergence is generally well-timed, and non-pollinators are relatively long-lived, so even if they emerged early, they would probably live long enough to reproduce.

The population structure of yuccas in space and time also plays a modest role in limiting exploitation. Extreme isolation of yuccas in space may consistently protect them from non-pollinator exploitation, but such isolation may also prevent them from being discovered by pollinators, resulting in a net loss of seed production. Isolation in time, on the other hand, plays more of a role in shifting non-pollinator activity onto inflorescences of different ages in different years, than in limiting exploitation. In years when non-pollinators emerge early, the oldest fruit on the site are most vulnerable to attack, which allows the youngest fruit on the site to escape. Conversely, when moths emerge late, the oldest fruit on the site will escape oviposition, and the younger fruit will be at risk. Because exploitation by the non-pollinating moth is strongly dependent on the environment into which it emerges, and that environment changes from year-to-year, there is probably no consistent escape from exploitation, and therefore no selection for yuccas which bloom early or late in the season.

What limits exploitation of the yucca-yucca moths system, then, if intraspecific competition and spatial and temporal and spatial isolation play such a limited role? In this study, the only consistently strong limit to exploitation was interspecific competition between the larvae of pollinators and non-pollinators. In as many as 35% of the locules in all yucca fruit at Old 89, there are enough pollinators to reduce non-pollinator survivorship by 80%. I conclude that in this system, it is one of the mutualists - the pollinating moths - that limit exploitation and drives the coexistence of yuccas, pollinators, and their exploiters.

Literature Cited

Addicott, J. F. 1996. Cheaters in yucca/moth mutualism. *Nature (London)* 380: 114-15.

Addicott, J. F., J. Bronstein, and F. Kjellberg. 1990. Evolution of Mutualistic Life-Cycles: Yucca Moths and Fig Wasps. *Insect Life Cycles.* 1 ed., Editor Francis Gilbert, 143-61. London: Springer-Verlag.

Alexandersson, R. and J. Agren. 1996. Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. *Oecologia* 107, no. 533-540.

Biere, A. and S. J. Honders. 1996. Impact of flowering phenology of *Silene alba* and *S. dioica* on susceptibility to fungal infection and seed predation. *Oikos* 77, no. 3: 467-80.

Bronstein, J. L. 1991. The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? *Oikos* 61: 175-86.

Bultman, T. L. and P. L. Mathews. 1996. Mycophagy by a millipede and its possible impact on an insect-fungus mutualism. *Oikos* 75, no. 67: 74.

Fuller, O. S. 1990. "Factors affecting the balance of cooperation and conflict between the yucca moth, *Tegeticula yuccasella* and its mutualist, *Yucca glauca*." University of New Mexico.

Holmes, H. B. 1972. Genetic evidence for fewer progeny and a higher percent males when *Nasonia vitripennis* oviposits in previously parasitized hosts. *Entomophaga* 17: 79-88.

Inouye, D. W. 1983. The ecology of nectar robbing. *The Biology of Nectaries.* editors B. Bentley and T. Elias, 153-73. New York: Columbia University Press.

Ives, A. R. 1989. The optimal clutch size of insects when many females oviposit per patch. *The American Naturalist* 155, no. 5: 671-87.

Janzen, D. H. 1975. *Pseudomyrex nigropilosa*: A parasite of a mutualism. *Science* 183: 936-37.

Letourneau, D. K. 1990. Code of ant-plant mutualism broken by parasite. *Science* 248: 215-17.

———. 1991. Parasitism of ant-plant mutualisms and the novel case of *Piper*. *Ant-Plant Interactions* Chapter 25: 390-418.

Louda, M. 1982. Inflorescence spiders: A cost-benefit analysis for the host plant *Haplopappus venetus* Blake (Asreraceae). *Oecologia* 55: 185-91.

Morris, W. F. 1996. Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology* 77, no. 5: 1451-62.

Parker, G. A. and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *The American Naturalist* 128: 573-95.

Pellmyr, O. and C. J. Huth. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature (London)* 372: 257-60.

Pellmyr, O., J. Leebens-Mack, and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-56.

Powell, J. A. 1989. Synchronized, mass-emergencies of a yucca moth, *Prodoxus y-inversus* (Lepidoptera:Prodoxidae), after 16 and 17 years in diapause. *Oecologia* 81, no. 4: 490-493.

Prys-Jones, O. E. and P. G. Willmer. 1992. The biology of alkaline nectar in the purple toothwort (*Lathraea clandestina*): ground level defences. *Biological Journal of the Linnean Society* 45: 373-88.

Richter, K. S. and A. E. Weiss. 1995. Differential abortion in the yucca. *Nature (London)* 376: 557-58.

Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63, no. 2: 354-60.

Roubik, D. W., Holbrook N. M. and German P. V. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161-67.

Skinner, M. C. and J. Mandracchia. 1985. Clutch size as an optimal foraging problem for insect parasitoids. *Ecological Entomology* 17: 231-38.

Soberon Mainero, J. and C. Martinez del Rio. 1985. Cheating and taking advantage in mutualistic systems. *The Biology of Mutualism.* editor D. H. Boucher, 192-216. London: Croom Helm.

Stephenson, A. G. 1981. Toxic nectar deters nectar thieves of *Catalpa speciosa*. *The American Midland Naturalist* 105, no. 2: 381-83.

———. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *Journal of Chemical Ecology* 8, no. 7: 1025-34.